UNIVERSITY OF ARIZONA
39001007201703

CONTRIBUTIONS

FROM THE

LABORATORY OF VERTEBRATE

BIOLOGY

Numbers 51 to 65

(1952-1954)

Ann Arbor

UNIVERSITY OF MICHIGAN PRESS

The *Contributions from the Laboratory of Vertebrate Biology* are issued at irregular intervals by the Institute of Human Biology, University of Michigan.

Univ. of Arizona Library

CONTENTS

Number

51. Preliminary studies on the vegetation of an old-field community in southeastern Michigan. Francis C. Evans and Stanley A. Cain. (17 pp., 2 pls., 2 figs. March, 1952.)

52. The distribution patterns of three plant species in an old-field community in southeastern Michigan. Stanley A. Cain and Francis C. Evans. (11 pp., 3 figs., 1 map. March, 1952.)

53. Measures of plant aggregation based on contagious distribution. George W. Thomson. (16 pp. March, 1952.)

54. The influence of size of quadrat on the distributional patterns of plant populations. Francis C. Evans. (15 pp., 1 fig. March, 1952.)

55. Measure of the spacing between individuals within a population. Lee R. Dice. (23 pp., 13 figs. March, 1952.)

56. An experimental study of habitat selection by prairie and forest races of the deermouse, *Peromyscus maniculatus*. Van T. Harris. (53 pp., 2 pls., 1 fig. May, 1952.)

57. Variation in body dimensions and pelage color of certain laboratory-bred stocks of the *Peromyscus truei* group. Lee R. Dice. (26 pp., 3 figs. June, 1952.) ✓+

58. Water requirements of certain rodents from xeric and mesic habitats. Robert G. Lindeborg. (32 pp., 3 figs. June, 1952.)

59. The measurement of fertility and its use as an index of reproductive isolation among certain laboratory stocks of *Peromyscus*. T. T. Liu. (12 pp. February, 1953.) ✓

60. Prenatal mortality in *Peromyscus* with special reference to its bearing on reduced fertility in some interspecific and intersubspecific crosses. T. T. Liu. (32 pp., 1 pl., 3 figs. February, 1953.) ✓+

61. Arboreal adaptations of *Peromyscus*, with special reference to use of the tail. B. Elizabeth Horner. (77 pp., 7 pls. February, 1954.) ✓+

62. The statistical concept of home range as applied to the recapture radius of the deermouse (Peromyscus). Lee R. Dice and Philip J. Clark. (15 pp., 2 figs. February, 1953.)

63. Ants of an old-field community on the Edwin S. George Reserve, Livingston County, Michigan. Mary Talbot. (13 pp. April, 1953.)

64. The soil arthropods of a field in southern Michigan: A study in community ecology. Nelson G. Hairston and George W. Byers. (37 pp., 26 figs. February, 1954.)

65. A description of a subhumid corridor across northern Central America, with comments on its herpetofaunal indicators. L. C. Stuart. (26 pp., 6 pls., 6 maps. March, 1954.)

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

University of Michigan, Ann Arbor, Michigan

Number 51 March, 1952

PRELIMINARY STUDIES ON THE VEGETATION OF AN OLD-FIELD COMMUNITY IN SOUTHEASTERN MICHIGAN

By FRANCIS C. EVANS and STANLEY A. CAIN

Accepted for publication February 12, 1951

CONTENTS

Introduction 1
General Description of Field 3
Floristic Composition 5
Community Dynamics 15
Summary 16
Literature Cited 16

INTRODUCTION

THE community has long been recognized as a natural unit of ecological organization, but its complexity is so great that our knowledge of community structure and function is little better than superficial. Yet there is need for a thorough understanding of the dynamics of communities and of the manner in which they are maintained as recognizable entities. The sudden and generally severe alterations in the dynamic balance of nature which are caused by the rapidly expanding influence of man upon his environment call for a renewed effort to investigate and to comprehend the numerous factors and forces which integrate and regulate communities.

A long-term project to study the complete biota and the organization and operation of a natural community was initiated in the summer of 1948 by the Laboratory of Vertebrate Biology of the University of Michigan. Among the ultimate objectives of this study are a description of the community in terms of its energy utilization and of its productivity as a biological system and a comprehension of the mechanisms involved in its maintenance as a natural unit. The development of satisfactory techniques to achieve these objectives will of necessity constitute an important part of the work. It is expected that the ideas and methods which arise from this study will be, at least in part, applicable to other types of communities.

Several criteria were held to be of importance in the selection of a community for these purposes. Such a community should be as free from present human disturbance as possible, and this freedom should be guaranteed for the duration of the study, however long that might be. The structure of the community should be relatively simple, for, in general, the less complex the community, the more easily can we discern its life processes. The nature of the surrounding environment must be taken into account, since the proximity of other different communities may have a profound effect upon the character of the unit under study. The size of area to be investigated is also important, for it must be small enough to be examined effectively, yet large enough to give representative and reliable results. Accessibility at all times of year would greatly facilitate an investigation of the sort contemplated here.

The most satisfactory combination of these conditions that was readily available was that provided by an abandoned field on the Edwin S. George Reserve, of the University of Michigan, Livingston County, Michigan, near the town of Pinckney and about 25 miles northwest of Ann Arbor. Through the generosity of the late Colonel George, a tract of approximately two square miles was given to the University in 1930 for the establishment of a natural-history reserve. Since 1928 it has been under game fence, free from fire or human interference with successional changes. In climate, physiography, and types of habitat it is representative of much of the surrounding region.

Descriptions of various aspects of the biology and ecology of the George Reserve have already been published (Blair, 1948; Burt, 1940; Cantrall, 1943; Howard, 1950; Rogers, 1942; Sutton, 1949). Cantrall (1943) has provided a general description of the area, together with an aerial photograph and a contour map. Much of this information has proved helpful in the preliminary stages of the investigation of the old-field community under study. The ecologist needs to call upon many specialists for assistance, not only for determination of the species with which he is dealing, but also concerning environmental features such as soil and quantitative techniques such as sampling methods.

The present paper is intended to be an introductory description of the vegetation of the field selected as a site for this study. It is the composition and structure of the vegetation which gives this community its characteristic appearance.

Acknowledgments

We are much indebted to J. Speed Rogers, Director of the Edwin S. George Reserve, for making the facilities of the Reserve available for this study. We should also like to thank Joyce H. Jones, William C. Steere, and Rogers McVaugh for determining and checking the identifications of lichens, mosses, and seed plants, respectively. Maurice W. Senstius very kindly identified the soil type and series for the samples obtained by Nelson G. Hairston and F. C. Evans. Victor J. Brookes, R. DeWitt Ivey, Dixon L. Riggs, and Fernando Segadas-Vianna assisted in taking samples of the vegetation, and Mrs. Emmy Hesz and D. L. Riggs weighed the material collected from the clipped quadrats. Lee R. Dice gave many helpful suggestions in the preparation of this manuscript.

GENERAL DESCRIPTION OF FIELD

The field under study is a 15-acre tract situated in the northeast quarter of section 19 of Putnam Township, lying a few hundred yards north of the Colonel George house, on a large glacial outwash plain in the central and highest part of the Reserve, at an elevation of 975 to 1000 feet. To the east of this plain is an esker-like formation, half-a-mile long, which is bordered by a series of kettle holes and deep depressions. These features are largely the result of the effects of ice and of the glacial waters of the ancestral Huron River drainage at the close of the Wisconsin glaciation. A diagram of the study area and its immediate environs is shown in Figure 1. The field is approximately 220 yards in width and 360 yards in length, and the long axis is oriented almost exactly due north.

History

The field is bordered on much of its periphery by oak-hickory woods. This same forest type evidently covered the field prior to clearing, which is believed to have been done early in the second half of the past century. Cultivation of the cleared fields on the uplands of the Reserve was carried on extensively before 1900 (Cantrall, 1943: 32). After the turn of the century these areas were increasingly given over to use as pastures, doubtless in part because of the generally sterile nature of the soil. For the past two decades, however, during which it has been under game fence as part of the Reserve, the field has not been subject to pasturing or other disturbance, although the maintenance of a sizable deer herd on the Reserve (O'Roke and Hamerstrom, 1948) has unquestionably been a factor in the slow rate at which the return to forest conditions is progressing.

Physiography

The present surface of the field has a gently rolling appearance, marked by a number of shallow depressions or swales which are concentrated largely in the northern half (Fig. 1). Approaching from the south, one encounters a slight rise culminating about mid-field and receding as gradually to the north. The ground slopes away sharply to the west and in the wooded area along the eastern margin. These slopes and swales determine the clearly marked drainage pattern. Several details of the field are shown in Plates I and II.

Climate

The present-day climate of the region in which the Reserve is located is a humid type characterized by low thermal efficiency and by

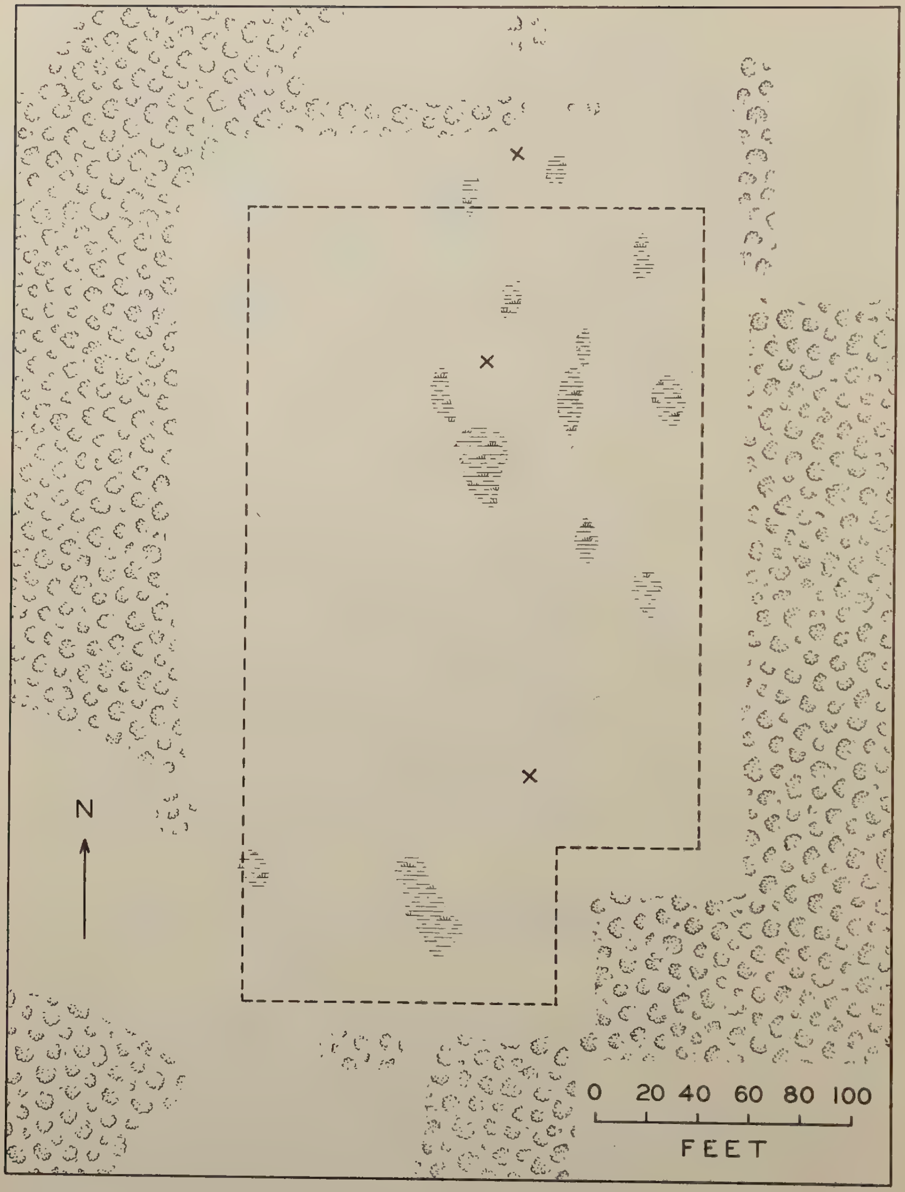


FIG. 1. Diagram of old field and environs, Edwin S. George Reserve, Livingston County, Michigan. X = single large hickories. Grassland represented by blank area. Dashed line indicates boundaries of study area.

Oak-hickory woods

"Swales"

rainfall throughout the year. This area lies on the boundary between the Dfb and the Dfa climatic zones of the Köppen system as revised by Ackerman (1941) for North America. In the Thornthwaite (1931) system, this climate is designated as BC'r. Data presented by Cantrall (1943) indicate the prevailing average annual precipitation to be about 30 inches and the range of mean monthly temperatures to be from approximately 22° F. in January to about 72° F. in June and July; the growing season is stated to be about 145 days. The exposed situation of the field makes it especially vulnerable to such weather extremes as strong winds, but as yet no detailed study of microclimates in the area has been made.

Soil

The soil that has developed under these conditions of physiography and climate is a gray-brown, podzolic, sandy loam belonging to the Fox series. Soil samples taken by N. G. Hairston and F. C. Evans showed that in the higher part of the field the dark-brown, organic horizon seldom exceeds a depth of 9 inches, whereas in the swales this same horizon extends as a thick phase to a depth of 2 or 3 feet. Beneath this dark-brown layer lies the B horizon, with a characteristic orange-red color resulting from the accumulation of ferric iron. The orange sand gradually gives way to a gray gravel which reaches a depth of at least 74 inches, the limits of our samples.

FLORISTIC COMPOSITION

Upon first sight the vegetation of the field appears to be more or less homogeneous and is clearly dominated by grasses. One is soon aware, however, of the existence of two principal community types, associated with the swales or depressions and the more elevated or upland areas of the field, respectively.

The swales, which are noticeably moister than the higher levels, support a dense growth of Poa pratensis, which forms a virtually closed community, although such forbs as Asclepias syriaca and Cirsium vulgare eventually gain footing. A conspicuous border of one or more species of Setaria is frequently found, completely or partly enclosing the swale. The vegetation in these depressions remains green long after the upland vegetation has dried up, and the contrast between the two is especially prominent in the late summer, though also conspicuous at other times of year (Pl. I, Fig. 1).

The major part of the vegetation is on the upland areas, which cover approximately 14.5 of the 15 acres occupied by the field. This community type is dominated by Poa compressa and the later-flowering Aristida purpurascens; interspersed with these are a number of other grasses, most notably several species of Panicum, and a considerable variety of associated forbs. Several of the latter, such as Antennaria neglecta and A. fallax, have more or less strongly developed vegetative reproduction and often occur in patches. Others like Liatris aspera are also definitely clumped even in the absence of obvious vegetative propagation, and still others are of sporadic or of more regular occurrence. The result is a community characterized by a marked patchwork or mosaic distribution of most of its component species.

These two community types are of general occurrence throughout the Reserve and the surrounding region. They evidently correspond to the "bluegrass meadow association" and the "bluegrass field association" as described briefly by Blair (1948). Table I lists the vascular plants and macroscopic cryptogams which have thus far been observed in the particular field under study. A total of 112 species is recorded. Most of these occur in the Poa-Aristida community of the upland parts of the field, and it is with this assemblage that the remainder of this paper is primarily concerned.

Species-Area Relationship

In order to determine the size of quadrat most satisfactory for sampling purposes, a plot of 2048 square meters, or approximately one-half acre, lying well within an apparently typical part of the Poa-Aristida community, was investigated October 22, 1948, with reference to species-area relationships. In one corner of this plot, a quadrat 0.25 square

TABLE I

A List of the Vascular Plants and Macroscopic Cryptogams Observed in an Old-field Grassland Community, Edwin S. George Reserve, Michigan

Nomenclature and sequence of names of lichens, mosses, and seed plants, according to Fink (1935), Steere (1947), and Fernald (1950), respectively.

LICHENS

Peltigera horizontalis (Huds.) Baumg.
Lecidea species
Cladonia sylvatica (L.) Hoffm.
Cladonia alpestris (L.) Rabenh.
Cladonia cristatella var. vestita Tuck.
Cladonia furcata var. racemosa (Hoffm.) Floerke
Cladonia cariosa (Ach.) Spreng.
Cladonia cornuta (L.) Schaer.
Cladonia pyxidata (L.) Hoffm.
Cladonia verticillata Hoffm.
Cladonia verticillata var. cervicornis (Ach.) Flot.
Parmelia sulcata Tayl.

MOSSES

Ceratodon purpureus (Hedw.) Brid.
Ditrichum pallidum (Hedw.) Hampe
Pleuridium subulatum (Hedw.) Lindb.
Bryum caespiticium Hedw.
Brachythecium species
Eurhynchium pulchellum (Hedw.) Dixon
Atrichum angustatum (Brid.) BSG
Polytrichum juniperinum Hedw.
Polytrichum piliferum Hedw.

TABLE I (Continued)

SEED PLANTS

Juniperus communis var. depressa Pursh
Juniperus virginiana L.
Poa compressa L.
Poa pratensis L.
Danthonia spicata (L.) Beauv.
Sporobolus vaginiflorus (Torr.) Wood
Agrostis alba L.
Agrostis scabra Willd.
Phleum pratense L.
Aristida purpurascens Poir.
Panicum capillare L.
Panicum depauperatum Muhl.
Panicum meridionale Ashe
Panicum lanuginosum Ell.
Panicum sphaerocarpon Ell.
Panicum oligosanthes var. Scribnerianum (Nash) Fern.
Setaria glauca (L.) Beauv.
Setaria viridis (L.) Beauv.
Cenchrus longispinus (Hack.) Fern.
Andropogon scoparius Michx.
Cyperus filiculmis var. macilentus Fern.
Carex Muhlenbergii var. enervis Boott
Carex Bicknellii Britt.
Carex pensylvanica Lam.
Carex species
Juncus tenuis Willd.
Carya ovalis (Wang.) Sarg.
Quercus rubra L.
Quercus velutina Lam.
Rumex Acetosella L.
Polygonum tenue Michx.
Anemone cylindrica Gray
Arabis hirsuta var. pycnocarpa (Hopkins) Rollins
Crataegus crus-galli L.
Crataegus species
Fragaria virginiana Duchesne
Potentilla arguta Pursh
Potentilla argentea L.
Potentilla recta L.
Potentilla simplex Michx. (?)
Rubus flagellaris Willd.
Prunus serotina Ehrh.
Medicago sativa L.
Desmodium illinoense Gray
Desmodium paniculatum (L.) DC.
Lespedeza virginica (L.) Britt.
Lespedeza capitata Michx.
Lespedeza hirta (L.) Hornem.
Vicia villosa Roth.
Oxalis stricta L.
Euphorbia corollata L.
Hypericum perforatum L.
Lechea villosa Ell.
Lechea stricta Leggett
Viola sagittata Ait.
Oenothera biennis L., or related species
Oenothera rhombipetala Nutt.
Apocynum androsaemifolium L.
Apocynum cannabinum L.
Asclepias syriaca L.
Lithospermum croceum Fern.
Monarda fistulosa L.
Blephilia hirsuta (Pursh) Benth.
Hedeoma pulegioides (L.) Pers.
Solanum species
Physalis heterophylla Nees
Verbascum Thapsus L.
Plantago aristata Michx.
Galium pilosum Ait.
Houstonia longifolia Gaertn.
Vernonia species
Liatris aspera Michx.
Solidago juncea Ait.
Solidago nemoralis Ait.
Solidago rigida L.
Solidago graminifolia (L.) Salisb.
Aster species
Erigeron strigosus Muhl.
Erigeron canadensis L.
Antennaria neglecta Greene
Antennaria fallax Greene
Gnaphalium obtusifolium L.
Ambrosia artemisiifolia L.
Rudbeckia hirta L.
Achillea Millefolium L.
Cirsium vulgare (Savi) Tenore
Krigia virginica (L.) Willd.
Tragopogon pratensis L.
Lactuca canadensis L.
Lactuca pulchella (Pursh) DC.
Hieracium Gronovii L.
Hieracium longipilum Torr.

decimeters in area was laid out and the species of plants present recorded. A quadrat double this size and including the first quadrat was next laid out and the species of plants present again listed. This procedure was repeated a number of times to provide a series of quadrats, each with an area twice that of the preceding one and containing all of the smaller quadrats. A transition from the quadrat of 64 square decimeters to one of 100 square decimeters facilitated the laying out of the larger quadrats. The complete series of 21 "nested" quadrats ranged in size from 0.25 to 204,800 square decimeters. Table II lists the species of plants which were observed in this series. The smallest quadrat contained but one species, Aristida purpurascens, while a total of 48 species was recorded for the largest quadrat.

Additional species-area data were obtained in June, 1949, when sets of nested quadrats ranging in size from one square decimeter to one square meter were used for sampling the Poa-Aristida community. A series of 20 such sets was taken in a systematic or regularized manner, the sets being spaced about 20 meters apart on a grid pattern. Another series was similar in all respects except that the locations of the sets were drawn at random. The number of species per quadrat for each set of these two series is shown in Table III. When each series is considered as a whole and the total number of species found in all quadrats of a given size is recorded, the results for the two series are comparable for all quadrat sizes except the two largest, which contained more species in the randomized series. The species-area curve (Cain, 1938) obtained by plotting number of species per quadrat against quadrat area is shown in Figure 2. The point on the curve which represents an increase of 10 per cent

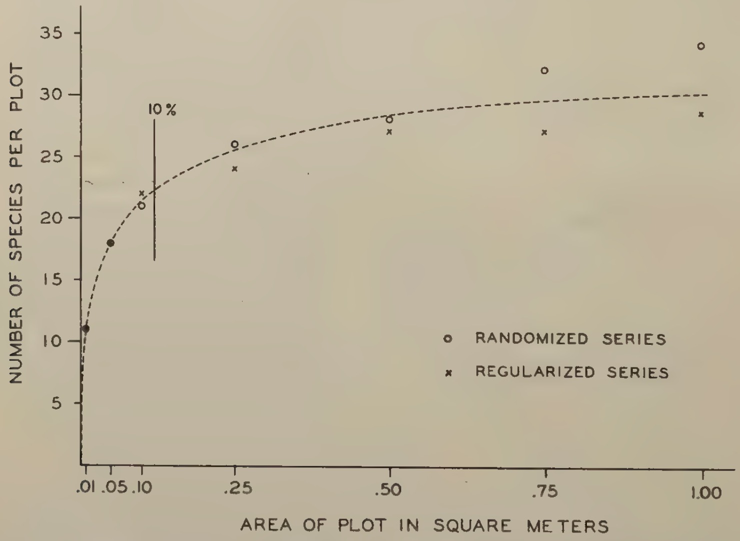


FIG. 2. Species-area relationships obtained from randomized and regularized series of nested plots, Poa-Aristida community, Edwin S. George Reserve, Livingston County, Michigan, June 7, 1949. Dashed line represents free-hand curve showing general trend of relationships. Vertical line indicates point on curve at which a 10 per cent increase in sample area gives an increase of 10 per cent in the total number of species sampled.

TABLE II

Occurrence of Plant Species in a Series of Nested Quadrats in a Poa-Aristida Community, Edwin S. George Reserve, October 22, 1948.

One quadrat only of each size examined. x, present; -, absent.

Species	Area in Square Decimeters																				
	0.25	0.50	1	2	4	8	16	32	64	100	200	400	800	1,600	3,200	6,400	12,800	25,600	51,200	102,400	204,800
Aristida purpurascens	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Rumex Acetosella	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Cladonia verticillata	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Cladonia cristatella	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Poa pratensis	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Poa compressa	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Peltigera horizontalis	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Cladonia cornuta	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Oxalis stricta	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x
Cladonia pyxidata	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x
Antennaria fallax	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x
Panicum meridionale	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x
Gnaphalium obtusifolium	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x
Ambrosia artemisiifolia	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x
Aster sp. (sterile rosette)	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x
Solidago rigida	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x
Liatris aspera	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x
Antennaria neglecta	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x
Polygonum tenue	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x
Solidago nemoralis	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x
Polytrichum piliferum	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x
Hieracium longipilum	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x
Hieracium Gronovii	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x
Panicum oligosanthes var. Scribnerianum	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x
Hedeoma pulegioides	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x
Lespedeza capitata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x
Ditrichum pallidum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x
Tragopogon pratensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x
Cyperus filiculmis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x
Monarda fistulosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x
Panicum depauperatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x
Cladonia cariosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x
Lactuca sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x
Polytrichum juniperinum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x
Panicum sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x
Oenothera biennis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x
Crataegus crus-galli	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x
Prunus serotina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x
Lechea villosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x
Lecidea sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x
Asclepias syriaca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x
Lespedeza virginica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x
Setaria glauca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Potentilla argentea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Juniperus communis var. depressa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Physalis heterophylla	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Crataegus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Cladonia alpestris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Total species	1	2	2	3	3	5	7	8	9	13	14	15	19	25	28	33	36	36	41	42	48

Univ. of Arizona Library

TABLE III

Species-Area Data from Twenty Randomized and Twenty Regularized Sets of Nested Quadrats Used in Sampling the Poa-Aristida Community, Edwin S. George Reserve, June 7, 1949

Number of Species Per Quadrat															
Randomized Series								Regularized Series							
Plot Size (sq. m.)	0.01	0.05	0.10	0.25	0.50	0.75	1.00	Plot Size (sq. m.)	0.01	0.05	0.10	0.25	0.50	0.75	1.00
Plot Number								Plot Number							
1 . . .	3	3	3	4	5	5	6	1 . . .	2	4	4	5	6	7	7
2 . . .	3	6	7	8	8	10	12	2 . . .	2	3	5	7	10	11	12
3 . . .	3	4	5	8	8	9	10	3 . . .	3	9	11	12	12	14	15
4 . . .	1	4	5	7	7	8	9	4 . . .	3	5	6	9	10	10	13
5 . . .	3	8	8	9	9	11	12	5 . . .	4	5	6	7	7	8	9
6 . . .	1	4	4	5	6	6	8	6 . . .	2	6	7	9	10	11	13
7 . . .	4	7	8	9	9	11	11	7 . . .	4	4	4	5	7	8	9
8 . . .	3	5	5	6	9	9	10	8 . . .	2	4	4	6	6	9	9
9 . . .	2	5	6	7	8	10	10	9 . . .	1	4	7	10	13	15	15
10 . . .	4	6	7	8	11	11	11	10 . . .	3	6	7	8	9	11	11
11 . . .	4	6	6	8	10	12	12	11 . . .	3	4	5	6	8	8	10
12 . . .	2	5	5	7	8	8	10	12 . . .	1	4	4	7	8	8	8
13 . . .	3	5	7	10	11	11	13	13 . . .	3	3	5	5	6	6	6
14 . . .	3	4	5	5	7	8	10	14 . . .	3	5	6	7	8	9	9
15 . . .	3	4	6	7	8	9	9	15 . . .	2	5	6	8	9	9	10
16 . . .	3	7	9	11	13	14	14	16 . . .	3	3	4	5	7	8	8
17 . . .	3	4	6	8	10	10	12	17 . . .	3	4	4	5	5	5	7
18 . . .	2	5	5	5	6	7	8	18 . . .	3	4	4	4	6	6	6
19 . . .	3	4	7	12	12	14	15	19 . . .	3	4	5	7	9	10	10
20 . . .	3	6	7	9	11	11	11	20 . . .	2	4	5	6	7	7	7
Total species	11	18	21	26	28	32	34	Total species	11	18	22	24	27	27	28

of the total number of species sampled for an increase of 10 per cent of the total sample area is indicated by a vertical line crossing the curve. Whether one adopts this arbitrary measure proposed by Cain (1938) or relies on the point beyond which the curve flattens and tends to become asymptotic with the abscissa axis, a quadrat size of 0.25 square meters seems to be adequate for sampling this Poa-Aristida community as a whole, provided a sufficient number of samples is taken.

Frequency

Two additional randomized series of 0.25-square-meter quadrats were also collected in June, 1949. The percentage frequencies with which the various species occurred in the one regularized and the three randomized series are shown in Table IV. The results of these series are in general

TABLE IV

Comparison of Frequencies (in Per Cent) of Species from Different Sets of Sample Quadrats (0.25 sq. m. each) in the Grass-dominated Community of an Old Field on the Edwin S. George Reserve, June 6-7, 1949

	Regularized	Randomized Series 1	Randomized Series 2	Randomized Series 3
Number of plots	20	20	20	20
Poa compressa	95	100	100	100
Aristida purpurascens	90	90	80	75
Rumex Acetosella	100	95	100	90
Hedeoma pulegioides	55	80	75	65
Solidago nemoralis	75	70	65	70
Gnaphalium obtusifolium	50	40	30	50
Erigeron canadensis	25	35	35	50
Solidago rigida	20	30	30	15
Lespedeza capitata	10	5	10	5
Antennaria neglecta	25	25	20	15
Ambrosia artemisiifolia	5	10	15	20
Oxalis stricta	20	25	30	20
Potentilla arguta	...	...	...	5
Hieracium longipilum	20	15	25	20
Panicum oligosanthes var. Scribnerianum	...	15	30	20
Poa pratensis	5	30	20	20
Tragopogon pratensis	...	5	...	15
Asclepias syriaca	5	...	15	5
Oenothera rhombipetala	...	...	5	5
Liatris aspera	10	10	15	10
Panicum meridionale	5	10	20	5
Lespedeza virginica	10	...	5	10
Lechea villosa	...	...	...	5
Carex pensylvanica	...	10	...	5
Potentilla argentea	...	...	...	5
Panicum sp.	35	30	30	10
Cyperus filiculmis	...	...	...	10
Antennaria fallax	10	10	5	5
Krigia virginica	5	5	...	10
Solanum sp.	...	...	5	...
Carex sp.	...	5	5	...
Anemone cylindrica	...	5	...	...
Desmodium illinoense	...	5	...	...
Prunus serotina (seedling)	...	5	...	...
Fragaria virginica	5	...	...	...
Blephilia hirsuta	5	...	...	...
Lactuca sp.	5	...	...	...
No. spp. (Total 37)	24	26	24	29
Average percentage frequency	28.7	29.4	32.1	25.5

closely comparable. In nearly all cases the frequency percentages for the several species are of the same order of magnitude in the different sets of samples. Poa compressa and Aristida purpurascens have consistently high values. Rumex Acetosella was also widely encountered, but most of the individuals were small and depauperate. Species of intermediate frequency included Hedeoma pulegioides, Solidago nemoralis, Gnaphalium obtusifolium, and Erigeron canadensis. None of the other species found was encountered in more than 30 per cent of the quadrats sampled. These frequency values indicate the predominant influence of the two grasses in the community.

Biomass Determinations

The relative importance of P. compressa and A. purpurascens is also borne out by biomass determinations made during the summer and fall of 1949 and 1950. Nineteen 0.5-square-meter quadrats were clipped as close to the ground surface as possible. The air-dry weights in grams of the collected material are shown in Table V. P. compressa and

TABLE V

Biomass Determinations of Vegetation from Nineteen Clipped Quadrats (0.5 sq.m. each) in Poa-Aristida Community, Edwin S. George Reserve, Late Summer and Fall, 1949 and 1950

Species	Air-dry Weights (Grams) of Clipped Material		
	Total Weight	Wt./sq.m.	Per Cent of Total
Poa compressa	647.8	68.2	46.0
Aristida purpurascens	430.4	45.3	30.6
Rumex Acetosella	98.3	10.4	7.0
Solidago nemoralis	95.6	10.1	6.8
Other grasses	38.4	4.0	2.7
Danthonia sp.			
Panicum sp.			
Poa sp.			
Antennaria fallax and A. neglecta	22.6	2.4	1.6
Miscellaneous	74.6	7.8	5.3
Ambrosia sp.			
Cyperus sp.			
Erigeron sp.			
Gnaphalium sp.			
Hedeoma sp.			
Hieracium sp.			
Hypericum sp.			
Lactuca sp.			
Lespedeza sp.			
Liatris sp.			
Oxalis sp.			
Polygonum sp.			
Potentilla sp.			
Solidago sp.			
Total	1407.7	148.2	100.0

A. purpurascens greatly outweighed the remaining material and together composed 76.6 per cent of the total dry weight of the clippings. Rumex Acetosella and Solidago nemoralis were the only other species to exceed 5 per cent of the total weight. All other species taken together comprised less than 10 per cent of the total weight.

Density and Spacing

We have as yet made no effort to estimate the coverage for the various species of the Poa-Aristida community. Coverage is difficult to measure with a satisfactory degree of accuracy in mixed grass-forb communities. Information about the density of individual plants or culms was obtained from the clipped quadrats described above. The average numbers of individuals counted on these quadrats are shown in Table VI. P. compressa

TABLE VI

Counts of Individual Culms or Plants on Nineteen Clipped Quadrats (0.5 sq.m. each) in Poa-Aristida Community, Edwin S. George Reserve, Late Summer and Fall, 1949 and 1950

Species	Number of Individual Culms or Plants		
	Total Number	No./sq.m.	Per Cent of Total
Aristida purpurascens	5593	588.7	40.8
Poa compressa	5260	553.7	38.3
Rumex Acetosella	1745	183.7	12.7
Other grasses Danthonia sp. Panicum sp. Poa sp.	484	50.9	3.5
Antennaria fallax and A. neglecta	220	23.2	1.6
Solidago nemoralis	131	13.8	1.0
Miscellaneous Ambrosia sp. Cyperus sp. Erigeron sp. Gnaphalium sp. Hedeoma sp. Hieracium sp. Hypericum sp. Lactuca sp. Lespedeza sp. Liatris sp. Oxalis sp. Polygonum sp. Potentilla sp. Solidago sp.	286	30.1	2.1
Total	13,719	1444.1	100.0

and A. purpurascens each exceeded 500 culms per square meter and together comprised 79.1 per cent of all culms and plants on the quadrats. Rumex Acetosella was the only other species to exceed 10 per cent of the total, and all other species taken together composed only 8.2 per cent of the total.

Additional data on density and spacing were obtained from a 50-meter transect taken on June 8, 1949. A steel tape of 1-cm. width, calibrated in centimeters, was stretched through a representative part of the Poa-Aristida community. The position of each plant rooted under the tape was recorded to the nearest centimeter. This transect was a 1 by 5000 cm. strip, with an area of 0.5 square meters, equivalent to one of the clipped plots. The number of individual culms or plants encountered in the transect and the average distance between adjacent individuals is shown in Table VII. Again, P. compressa and A. purpurascens predominate; the former had an average spacing of 18.1 cm. between culms and the latter an average spacing of 19.3 cm. In neither species did the frequency distribution of spacing measurements fit a normal curve; 65.3 per cent of the Poa culms and 65.2 per cent of the Aristida culms were more closely spaced than the average found on the line. Nevertheless, Poa occurred in 96 per cent of the 1-meter subdivisions of the transect, and Aristida occurred in 100 per cent.

TABLE VII

Numbers of Individual Culms or Plants and Average Distances Between Adjacent Individuals Encountered Along a 50-meter Transect Through the Poa-Aristida Community, Edwin S. George Reserve, June 8, 1949

Species *	Number of Culms or Plants	Average Distance Between Adjacent Individuals (cm.)
Poa compressa	276	18.1
Aristida purpurascens	259	19.3
Rumex Acetosella	125	40.0
Antennaria neglecta	28	178.6
Antennaria fallax	25	200.0
Poa pratensis	16	312.4
Solidago nemoralis	11	454.5
Hedeoma pulegioides	10	500.0
Krigia virginica	5	1000.0
Panicum sp.	4	1250.0
Gnaphalium obtusifolium	3	1666.7
Erigeron canadensis	3	1666.7
Liatris aspera	2	2500.0
Hieracium longipilum	2	2500.0
Panicum oligosanthes var. Scribnerianum	2	2500.0

*Total species sampled = 15. Total area sampled = 0.5 sq.m.

COMMUNITY DYNAMICS

The mosaic character of the Poa-Aristida community has already been noted. As Watt (1947) pointed out, the significance of pattern in the plant community will be made clear only by an investigation of the processes and changes influencing the pattern. Although we have not yet attempted to make a detailed study of the dynamics of this old-field community, it seems desirable to accompany this preliminary description with a few brief notes on the evidence of succession.

Succession

The presence of scattered junipers, hawthorns, and cherry seedlings, and the marked ecotone with the adjacent oak-hickory woods (Pl. I, Fig. 2, and Pl. II, Fig. 1) are indicative of a general successional trend towards deciduous forest. The rate of succession, however, is slow in comparison with that observed on abandoned fields elsewhere (Thomson, 1943). Probable factors in the retardation of this succession include the general sterility of the soil and the marked effects of over browsing by the herd of deer maintained on the Reserve.

Microsuccessional Cycles

Within this general framework of slow succession there appear to be more rapid microsuccessional changes which repeat themselves over and over. The cycle of these changes bears much similarity to the "regeneration complex" of Watt (1947). The Poa-Aristida community seems to include a characteristic developmental pattern of local phases, marked by pioneer, building, mature, and degenerating stages, with the consolidated grass patches representing the mature stage of cycle.

One conspicuous cycle is apparently initiated by the development of patches of mosses, especially Ceratodon purpureus or Polytrichum piliferum, which invade bare areas and eventually form considerable colonies. Highly social species, such as Antennaria fallax and A. neglecta, may also be among the pioneers and form many solid, often circular, microstands up to one or two meters in diameter (Pl. II, Fig. 2). The building stage is characterized by the invasion of these patches by Rumex Acetosella and Poa compressa, and scattered individual seedlings of other grasses and forbs also appear. As the patch approaches maturity the grasses become the dominant plants. Degeneration sets in with the accumulation of many dead culms and stems, which are rapidly covered by Cladonia plants of several species. The end of the degenerative stage is marked by the occurrence of very local erosion planes, produced by the joint action of such forces as precipitation, frost, and wind. Such planes often have the erect cormlike rootstalks of dead Cyperus filiculmis standing exposed above the level of the bare soil, which is then a few centimeters lower than its original surface. These bare areas are, in turn, the sites of invasion by mosses, various seedlings of forbs, and eventually by the dominant grasses, thus repeating a more or less consistent sequence of events.

Such cycles give the appearance of self-perpetuating systems, at least from a short-term point of view. They are also frequently initiated by the activities of ants, ground squirrels, and other animals which bring considerable quantities of soil to the surface and destroy the previously existing vegetation. The community will not be thoroughly understood until the various processes involved in this sequence are worked out and until the reciprocal relations of plants, animals, and soil are fully explored.

SUMMARY

An abandoned field on the Edwin S. George Reserve, of the University of Michigan in southeastern Michigan, is being investigated to study the organization and operation of a natural community. Two principal community types are recognized within the field: a dense growth of Poa pratensis, which characterizes the hollow depressions or swales, and the vegetation of the upland areas, which is dominated by Poa compressa and Aristida purpurascens. Studies of frequency, biomass, density, and spacing indicate that the prevailing vegetation of the field is a secondary grassland, with which are associated various species common in this region to such comparatively sterile, exposed habitats. Most of the plants of the Poa-Aristida community of the upland areas in the field show some tendency towards clumping, and the mosaic or patchwork character of the vegetation is clearly evident. There is a slow successional trend towards deciduous forest, which formerly covered the field and which now adjoins it along much of its periphery. Within the framework of succession there appear to be more rapid microsuccessional changes, which repeat themselves over and over in the form of a cycle, marked by pioneer, building, mature, and degenerating stages, with the established grasses representing the mature stage.

LITERATURE CITED

ACKERMAN, E. A.

1941 The Köppen classification of climates in North America. Geog. Rev., 31: 105-11.

BLAIR, W. F.

1948 Population density, life span, and mortality rates of small mammals in the blue-grass meadow and blue-grass field associations of southern Michigan. Amer. Midl. Nat., 40: 395-419.

BURT, W. H.

1940 Territorial behavior and populations of some small mammals in southern Michigan. Misc. Publ. Mus. Zool. Univ. Mich., 45: 1-58.

CAIN, S. A.

1938 The species-area curve. Amer. Midl. Nat., 19: 573-81.

CANTRALL, I. J.

1943 The ecology of the Orthoptera and Dermaptera of the George Reserve, Michigan. Misc. Publ. Mus. Zool. Univ. Mich., 54: 1-182.

FERNALD, M. L.

1950 Gray's manual of botany. 8th rev. ed.; New York: Amer. Book Company.

FINK, B.

1935 The lichen flora of the United States. Ann Arbor: Univ. Mich. Press.

HOWARD, W. E.

1950 Dispersal, amount of inbreeding, and longevity in a local population of prairie deermice on the George Reserve, southern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 43: 1-50.

O'ROKE, E. C., and F. N. HAMERSTROM, JR.

1948 Productivity and yield of the George Reserve deer herd. Journ. Wildlife Mgt., 12: 78-86.

ROGERS, J. S.

1942 The crane flies (Tipulidae) of the George Reserve, Michigan. Misc. Publ. Mus. Zool. Univ. Mich., 53: 1-128.

STEERE, W. C.

1947 The bryophyte flora of Michigan. Papers Mich. Acad., 31 (1945): 33-53.

SUTTON, G. M.

1949 Studies of the nesting birds of the Edwin S. George Reserve. Part I. The vireos. Misc. Publ. Mus. Zool. Univ. Mich., 74: 1-37.

THOMSON, J. W., JR.

1943 Plant succession on abandoned fields in the central Wisconsin sand plain area. Bull. Torrey Bot. Club, 70: 34-41.

THORNTHWAITE, C. W.

1931 The climates of North America according to a new classification. Geog. Rev., 21: 133-655.

WATT, A. S.

1947 Pattern and process in the plant community. Journ. Ecology, 35: 1-22.

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price $0.50.

PLATE I

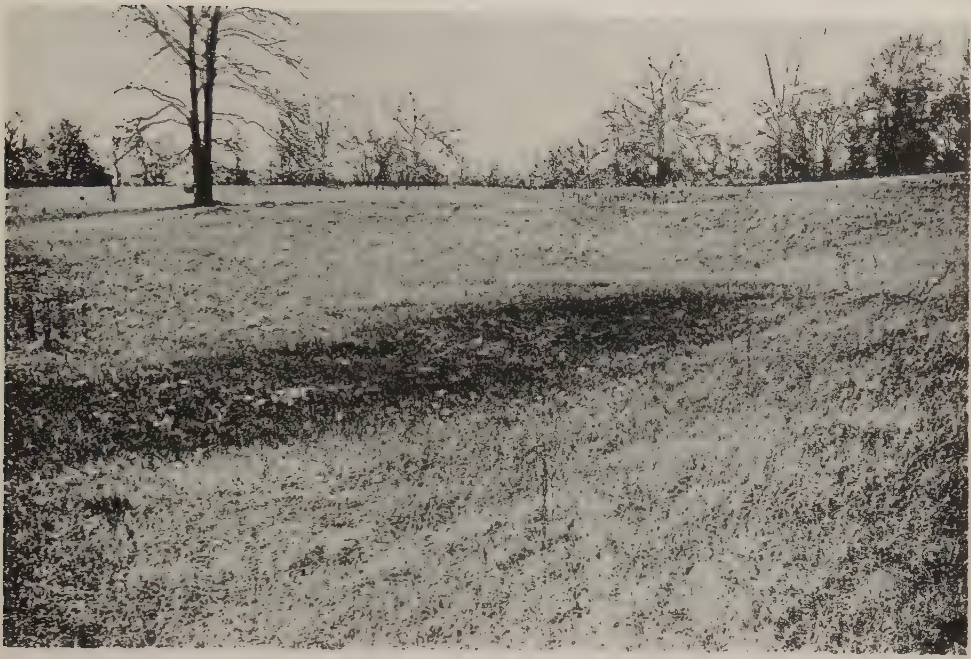


FIG. 1. Looking northwest from mid-field. The darker vegetation of a swale is seen in the center. E. S. George Reserve, March 19, 1949. S. A. Cain.

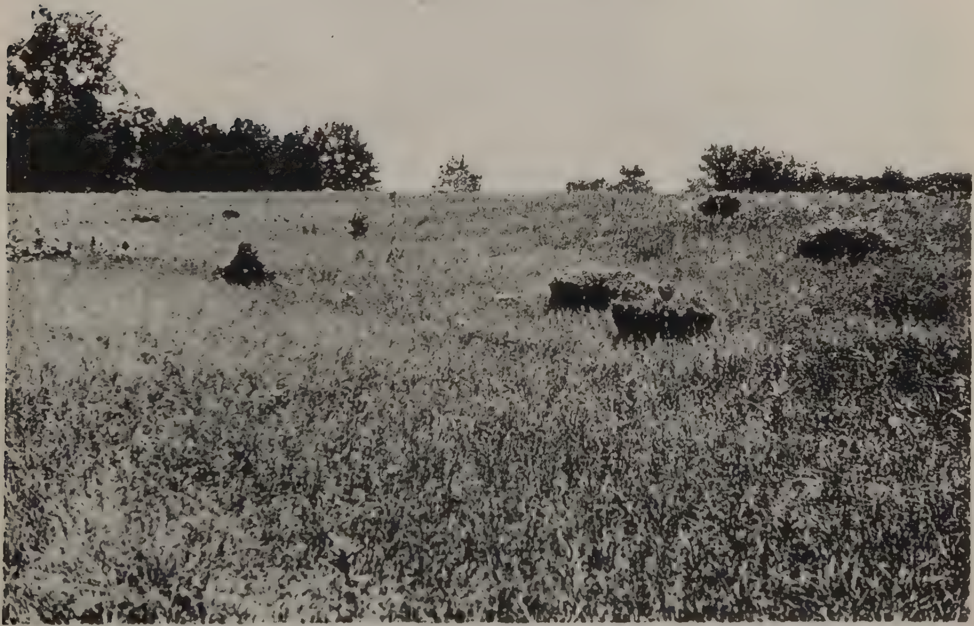


FIG. 2. Looking southwest from northern half of field. Note scattered junipers and hawthorns. E. S. George Reserve, August 3, 1949. F. C. Evans.

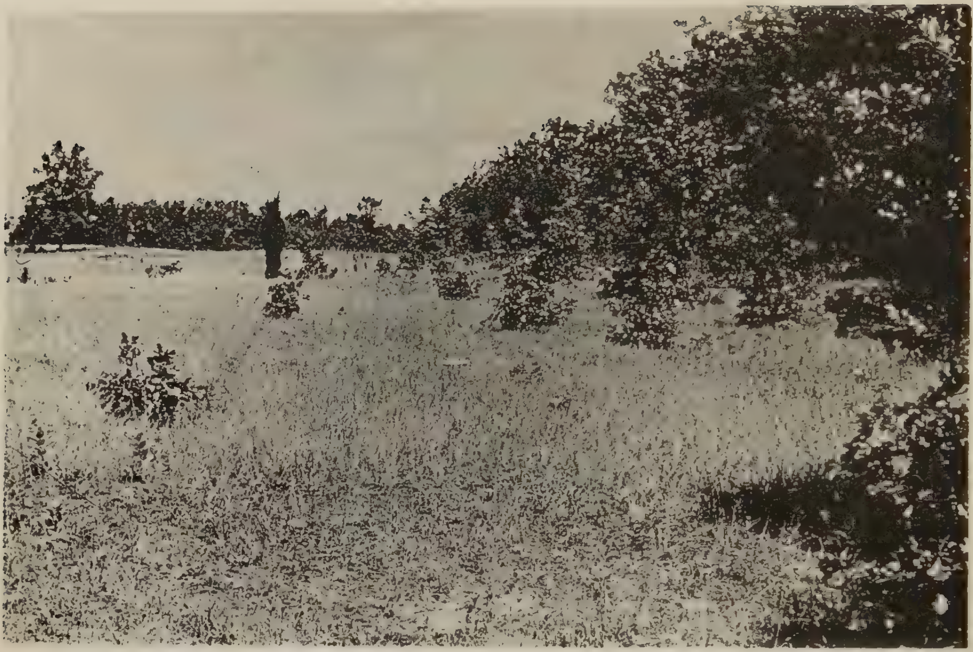


FIG. 1. Looking north along eastern margin of field, showing ecotone between field and oak-hickory woods. E. S. George Reserve, July 27, 1949. F. C. Evans.

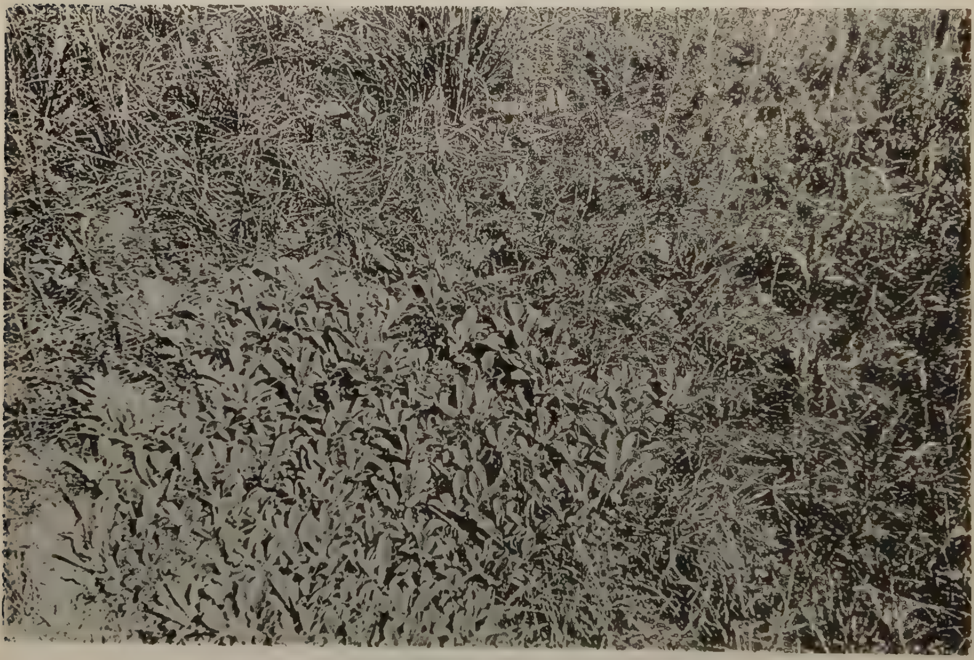


FIG. 2. Detail of vegetation, showing patch of *antennaria fallax*. E.S. George Reserve, August 3, 1949. F. C. Evans.

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

University of Michigan, Ann Arbor, Michigan

Number 52 March, 1952

THE DISTRIBUTION PATTERNS OF THREE PLANT SPECIES IN AN OLD-FIELD COMMUNITY IN SOUTHEASTERN MICHIGAN

By STANLEY A. CAIN and FRANCIS C. EVANS

Accepted for publication February 12, 1951

CONTENTS

Introduction 1
Material 4
Methods 4
Phytosociological Data 6
Description of Distribution Patterns 6
Discussion 9
Summary 10
Literature Cited 11

INTRODUCTION

AS part of a long-term project to study the organization and operation of a natural community, we have recently published a preliminary description of the vegetation of an abandoned field on the Edwin S. George Reserve of the University of Michigan, Livingston County, southeastern Michigan (Evans and Cain, 1952). In this description attention was called to the mosaic or patchwork character of the community. The spatial organization and structure of a community are in part the result of the distribution patterns exhibited by its component species. In the majority of natural situations, regular or truly random distributions of individuals are rare. On the contrary, species populations generally show varying degrees of aggregation or clumping, of the type that has become known as "contagious" distribution. The result is that few communities are perfectly homogeneous throughout their extent, but present instead a series of patches which, in turn, have a distributional pattern of their own.

Knowledge of patterns of distribution is necessary, not only to the community ecologist, but also to the population geneticist, who wishes to describe the degree of isolation from other individuals and populations as well as the possibilities for exchange of genetic material through interbreeding. The description, in adequate quantitative as well as qualitative terms, of the patterns of distribution displayed by the various species and by the community as a whole presents a difficult and frustrating problem, but one whose solution is desirable if one is to have a clear picture of community structure.

Information about distribution patterns may be obtained by various sorts of sampling procedure. For example, recent studies by Archibald (1948) and Thomas (1949) have attempted to describe distribution in terms of the frequency of occurrence in quadrats of uniform size. By recording the number of individuals present in each quadrat, one obtains the number of quadrats with 0, 1, 2, or more individuals, and these data can then be tabulated as a frequency distribution. This procedure is considerably simpler and less laborious than mapping the exact location of every individual within the given population. The picture of the distribution which it produces, however, is a formalized one which conceals the true distribution pattern, for it fails to indicate the spatial relations within and between the quadrats from which the frequency data were derived. It is evident that the size of quadrat chosen for such sampling may have considerable effect upon the resulting distributional picture. In addition, since the exact distribution patterns are generally not available to the reader, it is impossible to evaluate the information obtained from the quadrat data; that is, it is impossible to determine the extent to which the synthetic picture conforms to reality.

We approached this problem by considering the distributional patterns of three plant species which are components of the old-field vegetation. The locations of individual plants were plotted on a map (Map 1), which was then subjected to analysis by means of quadrats (Figs. 1, 2, and 3). Although none of the three species was of major importance in the community, their size and conspicuousness, as well as the ease with which individuals could be distinguished, made them especially suitable for this study. Our interest lay more in the development of a satisfactory technique which might be applicable to other populations than in the particular patterns displayed by these species.

Acknowledgments

J. Speed Rogers, Director of the Edwin S. George Reserve, kindly made the facilities of the Reserve available to us for this study. The Cranbrook Institute of Science generously placed at our disposal both space and equipment to facilitate construction of the original map. Fernando Segadas-Vianna and Mrs. Emmy Hesz assisted us in the preparation of both map and charts. George W. Byers copied the map for publication. To all of these people and institutions we wish to express sincere thanks.

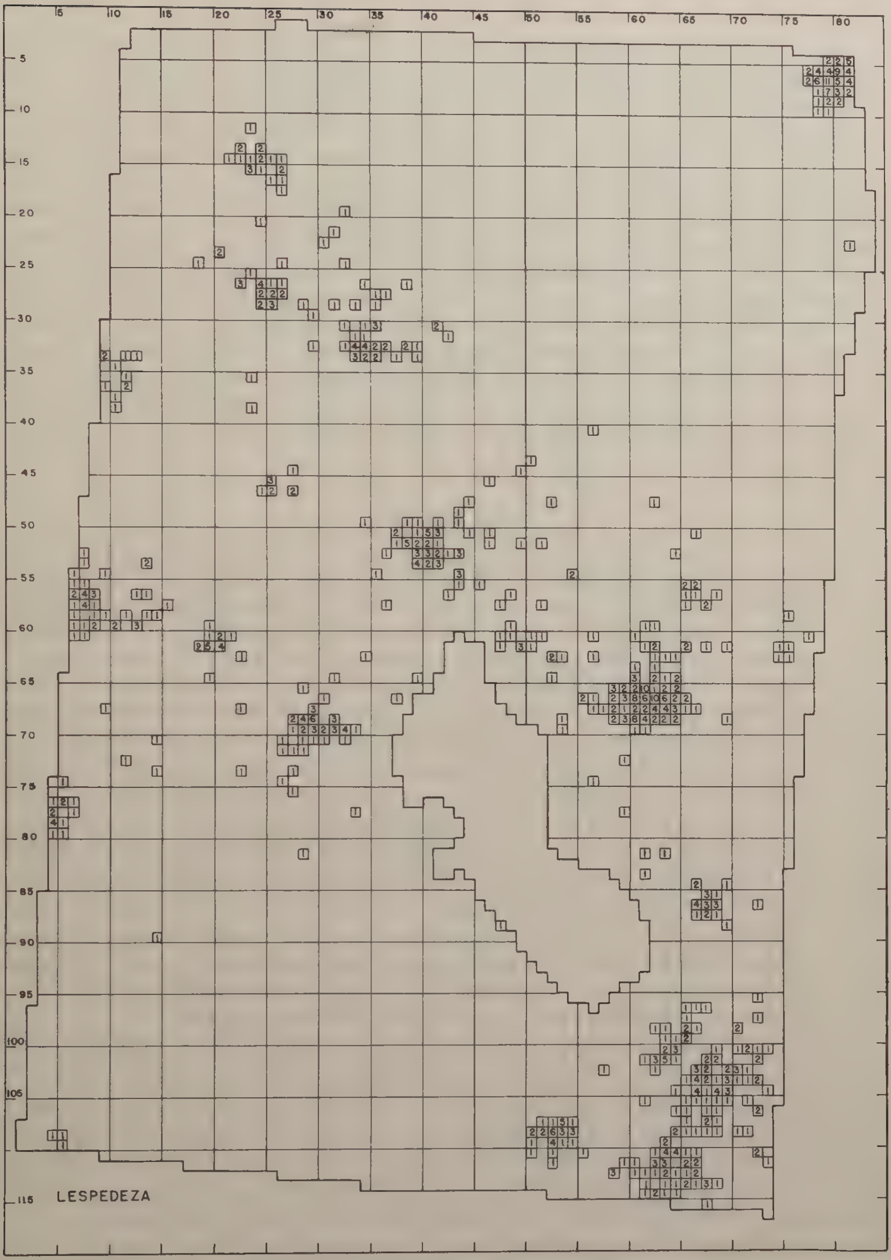


FIG. 1. Analysis of the Lespedeza capitata population given in Map 1, showing the numbers of individuals encountered in quadrats 1-meter square.

MATERIAL

The community in which this study was made consists of a secondary grassland dominated by two species, Poa compressa and Aristida purpurascens, with which are interspersed a number of other grasses as well as a considerable variety of forbs and shrubs (Evans and Cain, 1952). The species selected for mapping purposes were the bush clover, Lespedeza capitata, the blazing star, Liatris aspera, and the goldenrod, Solidago rigida. Each seemed to display a distribution pattern distinct from that of the others. The field data were taken between September 27 and October 3, 1949, at which time the flowering scapes of all three species were particularly prominent. We included as members of the populations only those plants which had one or more scapes in flower or which showed signs of having flowered during the season. Seedling plants were assigned to the next year's populations and were ignored for present purposes. All individuals conforming to the above population definition which were found in an area of approximately two acres were recorded.

METHODS

The positions of individual plants were obtained in the following manner. Reference points, in the form of wooden stakes, had previously been set up at about 20-yard intervals over the entire field, subdividing the area into large quadrats. Selecting one of these points, we placed a staff compass over it and took the compass bearing (accurate to 0.5 degrees) from that point to all individual plants of the three species which were located within the adjacent four quadrats. The distance of each plant from the point of reference was measured to the nearest centimeter with a steel tape. From this reference point, the bearing and distance were also taken for all of the other points marking the boundaries of the four quadrats. The compass and tape were then moved to the reference point which formed the center of a similar, contiguous block of four quadrats, and the procedure was repeated. In this manner an area of 7873 square meters was covered. Our basic data thus consisted of a bearing and distance from a point of reference for each individual plant of these three species within this area. This procedure was used because it is more rapid in the field than the plane-table survey method.

The data were then taken to the laboratory and, with the aid of a long, three-arm protractor and a rule, were plotted on a map. The reference points were established first, and the data referable to each point were then filled in. Each plant was represented by a symbol characterizing the particular species. A scale of 1 : 48 was used; that is, the distance of one foot in the field was represented as one-quarter inch on the map. With this scale it was possible to make a distinction between individuals which were as closely spaced as 6 inches apart. The entire map covered an area of about 5 by 7 feet and was made on pieces of heavy illustration board 30 by 40 inches each, so that smaller sections of the map could be examined separately. The whole map has been reproduced on a much smaller scale (Map 1).

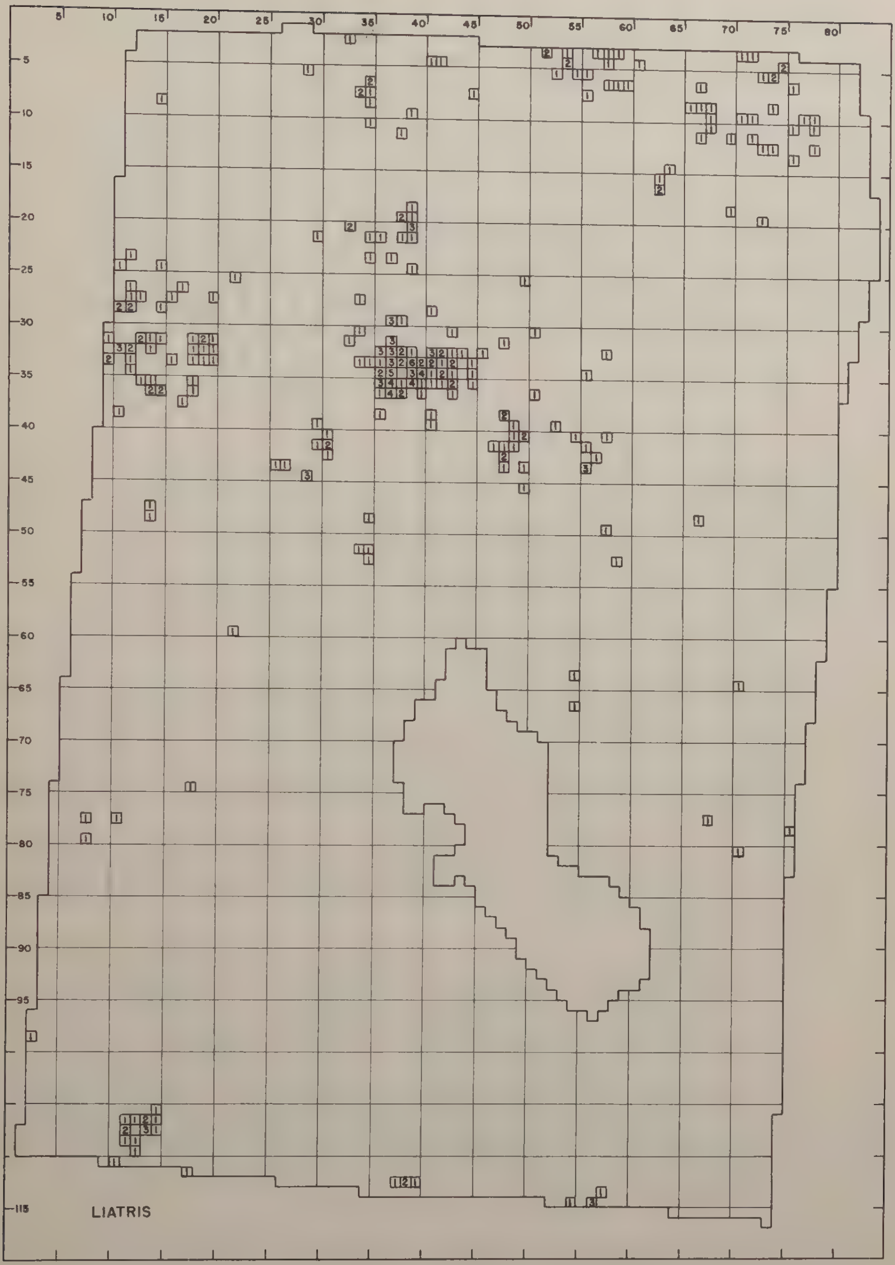


FIG. 2. Analysis of the Liatris aspera population given in Map 1, showing the numbers of individuals encountered in quadrats 1-meter square.

To analyze these distribution patterns, the entire mapped area was subdivided into smaller quadrats each 1-meter square. This was facilitated by covering the map with a transparent overlay sheet, on which there was a grid of meter-square quadrats on the same scale as the map. A chart was provided for each of the three species, on which was recorded the number of individual plants occurring in each meter-square quadrat (Figs. 1, 2, and 3). Quadrats in which no plants occurred were left blank. Those quadrats which did not lie completely within the boundaries of the map were not included on the charts. The total area charted amounted to 7640 square meters. Quadrats have been arranged in square blocks of 25 each, and co-ordinates, indicating the number of vertical columns and horizontal rows and corresponding to similar numbers on the map, have been provided to simplify the location of any given quadrat.

PHYTOSOCIOLOGICAL DATA

The populations of the three species under study which were present on the total area of 7640 square meters included on the charts were made up of 816 Lespedeza, 473 Solidago, and 320 Liatris plants, respectively. Density figures, in terms of the number of plants per square meter, are as follows: Lespedeza, 0.1068; Solidago, 0.0619; and Liatris, 0.0419. The mean area in square meters occupied by an individual plant was, therefore, 9.36 for Lespedeza, 16.15 for Solidago, and 23.88 for Liatris. The order of the species was somewhat different with respect to the frequency with which they occurred in the meter-square quadrats. The number of occupied quadrats was 462 for Lespedeza, 411 for Solidago, and 237 for Liatris, giving respective frequencies of 6.05, 5.38, and 3.10 per cent. Abundance values, expressed as the number of individuals per occupied quadrat, were 1.77 for Lespedeza, 1.35 for Liatris, and 1.15 for Solidago.

For each of these phytosociological characters, the relationships between the three species may be summarized by the following arrangement in order of decreasing values:

Density: Lespedeza > Solidago > Liatris
Mean area: Liatris > Solidago > Lespedeza
Frequency: Lespedeza > Solidago > Liatris
Abundance: Lespedeza > Liatris > Solidago

Each of these characters indicates something about the nature of the populations of these species, but taken separately they provide conflicting pictures of the patterns of distribution. Further description of these patterns is clearly desirable.

DESCRIPTION OF DISTRIBUTION PATTERNS

The tendency of the plants of these three species to occur as clumps is readily apparent. A considerable area in the lower center of the map and charts is seen to be altogether devoid of individuals. This area rep-

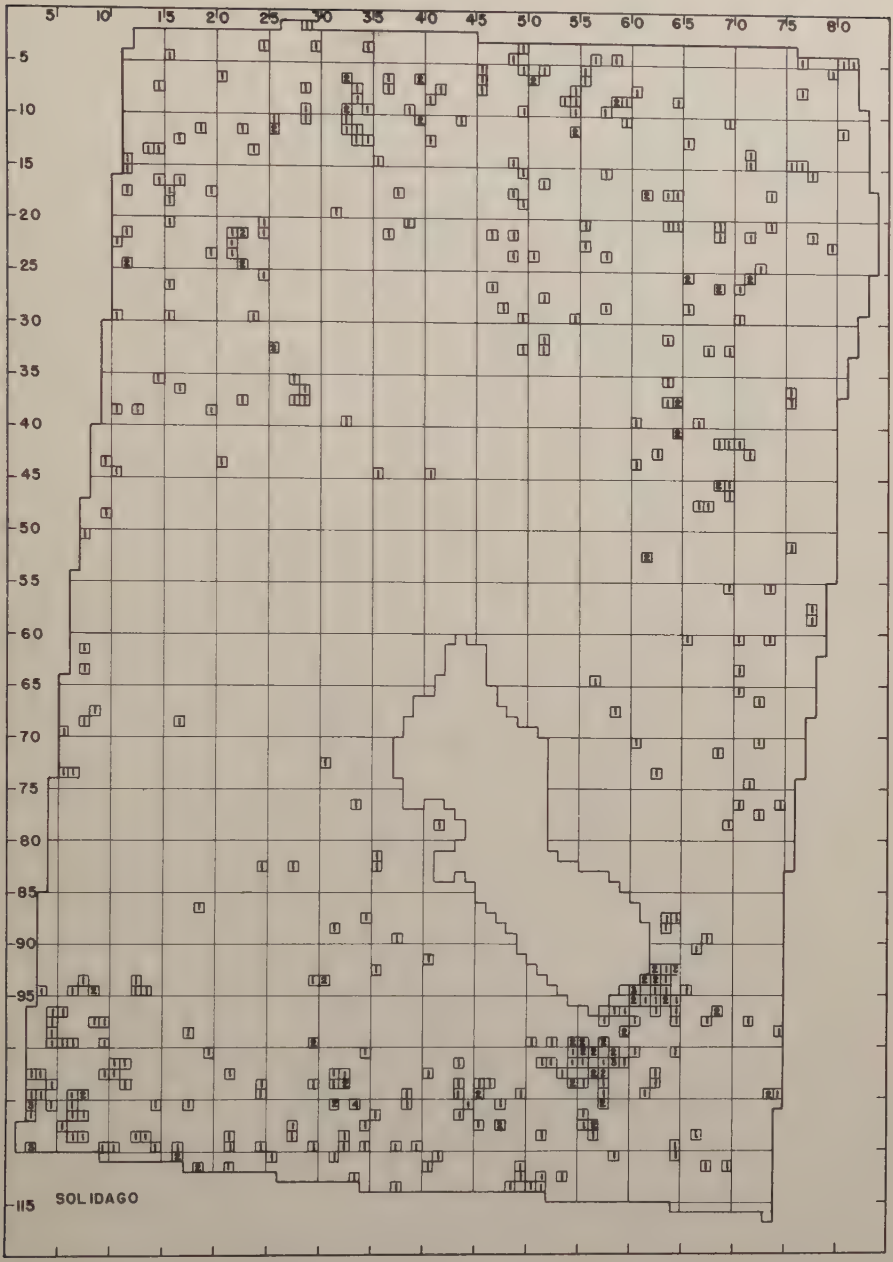
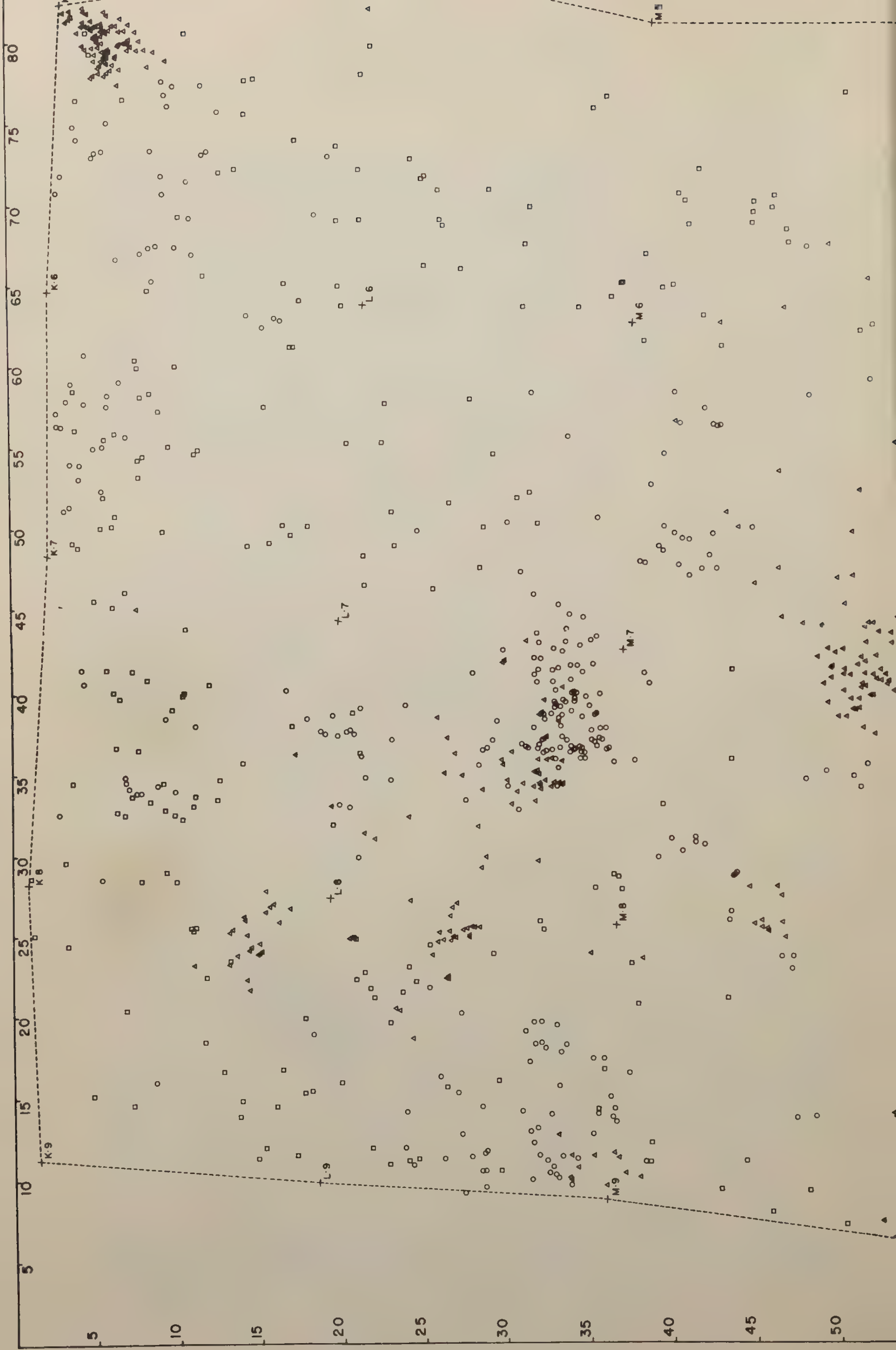
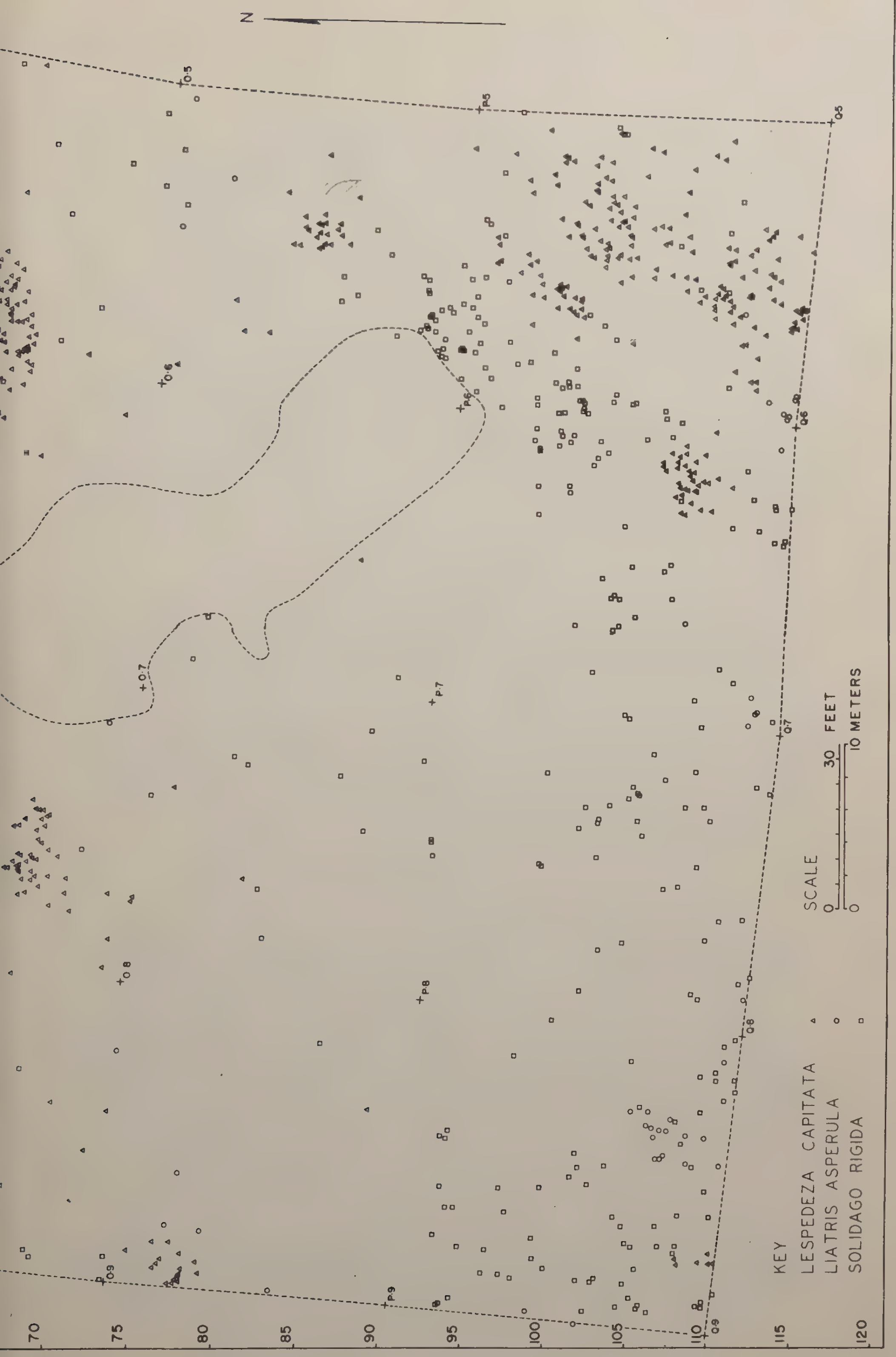


FIG. 3. Analysis of the Solidago rigida population given in Map 1, showing the numbers of individuals encountered in quadrats 1-meter square.



MAP 1. Locations of individual plants of Lespedeza of a grassland community, Edwin S. George Reserve, 3, 1949.



spera, and Solidago rigida in approximately two acres
Michigan, from field data taken September 27 - October

resents one of the shallow depressions or swales in the field, which were characterized by a dense growth of Poa pratensis sharply distinct from the P. compressa-Aristida purpurascens community found on the higher and drier levels (Evans and Cain, 1952). The three mapped species did not grow in this swale habitat at all, and the quadrats which were located wholly or partly therein were not included on the charts.

Casual inspection of the three charts reveals (1) the low order of density and frequency exhibited by these species, (2) the obvious tendency to clumping, which appears to be greatest in Lespedeza, least in Solidago, and intermediate in Liatris, and (3) the distinction between what may be called "major" clumps, consisting of large concentrations of closely-spaced individuals, and "minor" clumps, consisting of little groups of two, three, or four individuals each. The major clumps are probably due to clonal development resulting from vegetative reproduction or from localized seed dispersal, whereas the minor clumps may represent the beginnings of such clones or perhaps the chance associations resulting from random dispersal.

Lespedeza capitata

The distribution pattern for Lespedeza is marked by a strong development of major clumps, some fifteen of which may be recognized as wholly or partly within the boundaries of the chart. Minor clumps are poorly represented, and there are also relatively few isolated individuals or pairs. This species is clearly concentrated about centers of dispersal, which in turn do not appear to be randomly or evenly distributed but are grouped in a sort of diagonal belt running from upper left to lower right on the chart and leaving two conspicuously bare areas, one in the lower left corner and the other in the upper right.

Solidago rigida

Solidago, on the other hand, displays comparatively little evidence of major clumping. Only two or three aggregations of this type are apparent, and the individuals comprising these clumps are not as closely spaced as in Lespedeza . There is, however, a strong development of minor clumps and of scattered individuals and pairs. Distribution is much more nearly uniform in this species than in Lespedeza, and there is only one area that is largely devoid of individuals. The general impression is clearly one of a distribution approximating that of a randomly dispersed population.

Liatris aspera

A still different pattern is exhibited by Liatris. The over-all density and frequency are considerably less for it than for the other two species. As in Lespedeza, the majority of individuals are collected in major clumps, but not more than three or four of these are recognizable for Liatris, and the distances between clumps appear to be greater in Liatris than in Lespedeza. Liatris also shows more of a tendency to single individuals and pairs than does Lespedeza, but less than Solidago. Minor clumps are no more developed in Liatris than they are in Lespedeza. Unoccupied areas are comparable to those found in the Lespedeza pattern.

DISCUSSION

Ecologists have long sought for some satisfactory means of giving quantitative expression to such patterns of distribution, not only to obtain a better understanding of their structure, but also to facilitate comparison. Thomson (1952) has fitted the Lespedeza, Liatris, and Solidago distributions described above to several mathematical models in an attempt to determine the extent to which such models represent natural situations. Other authors (Clapham, 1936; Fracker and Brischle, 1944; McGinnies, 1934; Whitford, 1949) have tried to measure the extent to which certain population distributions depart from randomness, but none of the proposed measures has proved wholly reliable under all conditions, and their values are considerably affected by the size of quadrat used to obtain the frequency data, as is demonstrated elsewhere for the three populations discussed herewith (Evans, 1952). A new approach to the problem is provided by Dice (1952), who proposes a measure of the spacing among individuals within a population that is based upon the distance between adjacent plants, rather than upon data derived from quadrats.

The significance of a particular pattern of distribution can be understood only if one has a knowledge of the factors and processes that have produced it. The principal factors affecting the local distribution patterns of plant species may be subsumed under the headings of (1) microclimatic conditions, (2) edaphic variations, (3) the biology of the species concerned, particularly the methods of reproduction and dispersal, (4) the relations of the species to other organisms, animal as well as plant, occurring in the community, and (5) the element of chance in the dispersal and establishment of new individuals. Indeed, any description of a distributional pattern will itself be inadequate and lack meaning unless it can be interpreted in terms of process.

Lespedeza capitata possesses a slender, gradually tapering primary root which, under the conditions of the field, may extend to a depth of at least 36 inches and from which numerous branches develop. Excavation of Lespedeza plants having stems which were not more than 3 inches apart has failed to produce any evidence of connecting roots, and such closely-spaced individuals seem to have developed from separate seeds. Vegetative multiplication does not apparently play any part in the local distribution pattern of this species. This is true also for Liatris aspera, which has a cormlike tuber usually lying from 4 to 6 inches below the soil surface. Solidago rigida, on the other hand, possesses a shallow, creeping rhizome which develops lateral as well as terminal buds; as older parts of the rhizome die, the younger parts become separated and give rise to individual plants. It will be recalled that, although Solidago showed the least tendency toward major clumping, so far as these three species are concerned, it showed the greatest development of minor clumps, and it seems likely that this feature of its distribution pattern is largely due to rhizome spread.

There is also some evidence that the manner of seed dispersal has had its effect upon the patterns of distribution of these three species. The seeds of Lespedeza are heavier than those of Liatris or Solidago and, in contrast to these latter, are not equipped with a pappus for widespread aerial dispersal. Lespedeza seeds are therefore more likely to drop in the immediate vicinity of the parent plant. If a more limited seed distribution is actually the case with Lespedeza, this would help to explain the stronger tendency to major clumping displayed by this species. The closer approach to a random distribution demonstrated by Liatris and Solidago (Thomson, 1952) emphasizes the role that chance might be expected to play in the distribution of seeds by wind.

It would be premature at this point to try to evaluate the various factors responsible for these distributions. The complete absence of the three species from the swale habitat is suggestive of microclimatic and edaphic factors, or of competitive relationships to other plants, but further investigation of these aspects is required. More knowledge of the role of animals in the transportation of seeds is also needed. It is hoped that additional study of these and related factors will throw considerable light on the interpretation and significance of these patterns of distribution.

SUMMARY

The distribution patterns of populations of Lespedeza capitata, Liatris aspera, and Solidago rigida were obtained by taking the bearing and distance from a reference point of all individuals encountered in an area of approximately two acres. By means of these data, the location of each individual plant was plotted on a map. An overlay grid representing 1-meter-square quadrats was used to prepare frequency charts for the distribution of each species. Different relationships between the three species were indicated by the data for density, mean area, frequency, and abundance. The tendency to clumping appeared to be greatest in Lespedeza, least in Solidago, and intermediate in Liatris. A distinction was made between "major" clumps, which are probably due to clonal development resulting from localized seed dispersal or from vegetative reproduction, and "minor" clumps consisting of several individuals only, which may represent either the beginning of such clones or the chance associations resulting from random dispersal. The ability of Solidago to spread by rhizomes may account in part for the greater development of minor clumps in this species, while the possession of heavier seeds helps to explain the greater degree of major clumping in Lespedeza.

LITERATURE CITED

ARCHIBALD, E. A. A.

1948 Plant populations. I. A new application of Neyman's contagious distribution. Ann. Bot., 12: 221-35.

CLAPHAM, A. R.

1936 Over-dispersion in grassland communities and the use of statistical methods in plant ecology. Journ. Ecol., 24: 232-51.

DICE, L. R.

1952 Measure of the spacing between individuals within a population. Contrib. Lab. Vert. Biol. Univ. Mich., 55.

EVANS, F. C.

1952 The influence of size of quadrat on the distributional patterns of plant populations. Contrib. Lab. Vert. Biol. Univ. Mich., 54.

EVANS, F. C., and S. A. CAIN

1952 Preliminary studies of the vegetation of an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 51.

FRACKER, S. B., and H. A. BRISCHLE

1944 Measuring the local distribution of Ribes. Ecology, 25: 283-303.

McGINNIES, W. G.

1934 The relation between frequency index and abundance as applied to plant populations in a semi-arid region. Ecology, 15: 263-82.

THOMAS, M.

1949 A generalization of Poisson's binomial limit for use in ecology. Biometrika, 36: 18-25.

THOMSON, G. W.

1952 Measures of plant aggregation based on contagious distributions. Contrib. Lab. Vert. Biol. Univ. Mich., 53.

WHITFORD, P. B.

1949 Distribution of woodland plants in relation to succession and clonal growth. Ecology, 30: 199-208.

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price $0.20.

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

University of Michigan, Ann Arbor, Michigan

Number 53 March, 1952

MEASURES OF PLANT AGGREGATION BASED ON CONTAGIOUS DISTRIBUTION

By George W. Thomson

Accepted for publication February 12, 1951

CONTENTS

Introduction 1
Contagious Distributions Applied to Old-field Data 4
Measures of Clumping 6
Summary 8
Appendix: Calculation of Terms 9
Literature Cited 15

INTRODUCTION

THE distribution of plant species in plant communities has been studied from several different points of view, but few mathematical analyses of the problem have been made. The labor in the complete mapping of all the individuals of a single species in a community usually precludes this type of presentation and less satisfactory schemes must be used.

The usual method of obtaining quadrat frequency data on a single species is the sampling of a representative area of the community by a number of scattered areas (quadrats) and the determination of the number of plants of that species in each quadrat. If the plants are distributed completely at random over the area and they have no influence on each other it can be shown statistically that the distribution will be of the Poisson type (see below). This was established for a number of species in certain grassland communities by Blackman (1935) and by Ashby (1935). The presence of clones, rhizomes, and runners and other clumping factors, however, vitiates the fundamental assumptions and under these conditions the data do not follow a simple Poisson law. Among the workers who have studied the general problem of nonrandomness are Rommel (1930), McGinnies (1934), Ashby (1935, 1948), Blackman (1935, 1942), Clapham (1936), Fracker and Brischle (1944), Cole (1946), Archibald (1948), Whitford (1949), Thomas (1949), and Curtis and McIntosh (1950). Many of these investigators proposed measures of nonrandomness (see below), but the general problem of obtaining a measure of the size of the clumps was not taken up by them.

Two similar lines of approach to these nonrandom distributions are afforded by the use of "contagious" distribution functions such as those of Neyman (1939) and Thomas (1949), where the mathematical model assumes that primary centers ("clusters") are distributed at random and that individual plants are then distributed, again at random, about these primary centers. These models have proved more or less successful in representing certain plant-distribution data (Archibald, 1948; Thomas, 1949). A typical example of such an excellent agreement is provided by these authors for the distribution of Armeria maritima in an English marsh (Table I). This material is noteworthy in that both of these models fit satisfactorily the increase in the observed number of quadrats at two plants per quadrat. As can be seen, the simple Poisson series can not possibly fit this particular type of distribution.

TABLE I

Distribution of Armeria maritima

Plants Per Quadrat	Number of Quadrats			
	Observed	Calculated		
		Poisson*	Neyman †	Thomas ‡
0	57	20.6	54.9	57.0
1	6	32.5	7.9	6.0
2	12	25.7	10.1	10.1
3	5	13.5	9.0	9.5
4	5	5.4	6.5	6.5
5	5	1.7	4.3	4.1
6	7	0.5	2.8	2.6
7	1	0.1	1.8	1.6
8	0	0.0	1.1	1.0
9	1	0.0	0.9	0.6
10	1	0.0	0.4	0.3
11 and over	0	0.0	0.3	0.7
Total	100	100.0	100.0	100.0

* Poisson distribution (Thomas, 1949).

† Neyman's Type A contagious distribution (Archibald, 1948).

‡ Thomas' double Poisson series, Method II (Thomas, 1949).

The number of "plants per cluster" is one of the parameters of both these mathematical models. For the Armeria data the results are: Neyman, 2.39; Thomas, 2.68. These quantities are of the same magnitude and can be logically related to a small degree of clumping of the plants. In other words, the mathematical model appears to possess some relation to reality for this example. For Plantago maritima (Archibald, 1948; Thomas, 1949) a similar excellent agreement was found between the calculated series and the quadrat frequency data. The number of "plants per cluster" was found to be 2.16 (Thomas), again a reasonable value. Thomas pointed out, however, that although her mathematical set-up was so designed that the parameters of the distribution might be capable of physical interpretation, sufficient data were not then available to test whether the distribution parameters do, in fact, measure the actual number of "plants per cluster" and "clusters per quadrat."

A plot of the actual position of every plant of a given species in an area usually reveals some type of clumping or clustering which is quite evident to the eye but rather difficult to establish rigorously since the cluster boundaries are seldom distinct and it is difficult to tell where one cluster ends and another starts. An excellent example is shown by the position plots of several species in an old-field community on the Edwin S. George Reserve of the University of Michigan, Livingston County, southeastern Michigan. Cain and Evans (1952) have mapped and plotted the distribution patterns of Solidago rigida, Liatris aspera and Lespedeza capitata, as they occurred within an area of approximately two acres in this community. The number of plants in all the 7640 one-meter-square quadrats believed to be a valid part of the community are studied below. Casual observation of the position plots suggests that Liatris is more definitely clumped than Solidago and that Lespedeza is still more clumped.

The object of this study was to determine whether the clusters of the contagious series have any relation to these major clumps which are evident to the eye. The results strongly suggest that the clusters of these series are more closely related to the minor clumps or groups of plants that are immediately adjacent rather than to the evident clumps (Cain and Evans, 1952), and that one must look elsewhere for a simple statistical measure of the degree of major clumping which is evident to the casual observer. Such a measure may be related to the average spacing parameter described by Dice (1952).

Acknowledgments

The author acknowledges the assistance of Mrs. N. S. Peisner of the Ethyl Corporation in checking the coefficients in Tables VII and VIII and the advice and encouragement of Dr. S. A. Cain throughout the investigation.

This work was done in connection with the activities of the Herbarium Committee of the Cranbrook Institute of Science, Bloomfield Hills, Michigan, and is part of a larger program of investigation of the structure of a natural community, under the general direction of Dr. Francis C. Evans of the Laboratory of Vertebrate Biology of the University of Michigan.

CONTAGIOUS DISTRIBUTIONS APPLIED TO OLD-FIELD DATA

The observed frequency data for the three populations under consideration and the goodness of fit of the double Poisson series of Thomas to the values are shown in Tables II to IV. The values have been calculated by the two methods suggested by Thomas, the moment solution (her Method I) and the maximum likelihood solution (her Method II). By a mathematical coincidence the second method leads to an exact fit of the values for 0 and 1 plant per quadrat. Similar comparisons with Neyman's series are shown in Tables II and IV. The calculated values of the Neyman series in Table II are more strictly comparable to Method I, the moment solution of Thomas, since the constants of the Neyman series were also obtained by the method of moments. The application of the method of maximum likelihood to Neyman's Type A contagious distribution has been described by Shenton (1949). Unfortunately, the calculation is involved and requires the usual moment solution as an initial approximation. Table IV includes a comparison of the results by this method for the Lespedeza population.

The three species provide examples of an excellent fit (Solidago), a fair fit (Liatris), and a very bad fit (Lespedeza), but in all cases the size of the clusters of the Thomas model lies between 1 and 3 plants (average for the moment solutions, Method I: 1.6; average for the maximum likelihood solutions, Method II: 1.3). The size of the clusters of the Neyman model are 0.23 (Solidago) and 1.76 (Lespedeza) for the moment solutions. These values suggest that the Solidago distribution is

TABLE II

Distribution of Solidago rigida

Plants Per Quadrat	Number of Quadrats			
	Observed	Calculated		
		Thomas I	Thomas II	Neyman
0	7229	7230.5	7229.0	7229.7
1	356	351.9	356.0	354.2
2	49	52.2	50.0	50.1
3	5	5.0	4.6	5.4
4	1	0.4	0.4	0.5
5 or over . .	0	0.0	0.0	0.1
Total . . .	7640	7640.0	7640.0	7640.0
Plants per cluster	......	1.124	1.116	0.234
Clusters per quadrat	......	0.0551	0.0553	0.265
Plants per quadrat	......	0.0619	0.0617	0.0619

TABLE III

Distribution of Liatris aspera

Plants Per Quadrat	Number of Quadrats		
	Observed	Calculated	
		Thomas I	Thomas II
0	7403	7420.4	7403.0
1	183	140.0	183.0
2	34	62.3	46.7
3	14	14.4	6.5
4	4	2.4	0.7
5	1	0.4	0.1
6	1	0.1	0.0
7 or over	0	0.0	0.0
Total.	7640	7640.0	7640.0
Plants per cluster. .	......	1.436	1.243
Clusters per quadrat	......	0.0292	0.0315
Plants per quadrat. .	......	0.0419	0.0392

TABLE IV

Distribution of Lespedeza capitata

Plants Per Quadrat	Number of Quadrats				
	Observed	Calculated			
		Moment Solutions		Max. Likelihood Solutions	
		Thomas I	Neyman	Thomas II	Neyman*
0	7178	7279.2	7265.1	7178.0	7188.4
1	286	105.2	134.0	286.0	219.6
2	93	127.9	118.9	133.9	140.8
3	40	78.6	71.1	33.9	61.6
4	24	33.1	32.5	6.7	21.1
5	7	11.1	12.3	1.2	6.2
6	5	3.4	4.2	0.3	1.7
7	1	1.0	1.3		0.5
8	2	0.5	0.4		0.1
9	1		0.1		....
10	2		....		....
11	1		....		....
12 or over	0		....		....
Total	7640	7640.0	7640.0	7640.0	7640.0
Plants per cluster . .	....	2.208	1.756	1.448	1.252
Clusters per quadrat	....	0.0484	0.0608	0.0624	0.0853
Plants per quadrat. .	....	0.1068	0.1068	0.0903	0.1068

*Shenton's method.

more regular than random and that the Lespedeza is somewhat clumped and point up the difference between the results from the two contagious series models. It is evident that these clusters are very much smaller than the major clumps which are apparent to the eye on a casual observation of the plants themselves. If these species had been randomly distributed the number of plants per cluster would have been one, corresponding to the Poisson distribution. The divergence of this parameter from unity shows that the plants are not so distributed, but the nature and type of nonrandomness is not the same as the expectation suggested by the general appearance of the charts.

It is probable that the minor clusters of the mathematical models are only related to very local clumping conditions. This conclusion is partly confirmed by an examination of the position plot for Solidago, where a large number of very small clumps are evident; the major clumps are distinctive and easily differentiated from these local aggregates (see also Cain and Evans, 1952).

MEASURES OF CLUMPING

A number of authors have considered the general problem of measures of clumping without any marked degree of success. Much of the recent literature on phytosociological characters has been summarized by Curtis and McIntosh (1950), who consider at length the meaning and meanings of the fundamental terms such as frequency (proportion of quadrats containing species to total quadrats), density (individuals per unit area), mean area (area per individual), and abundance (density divided by frequency). They did not make a detailed study of nonrandomness for their synthetic population, although they discovered that the measures of nonrandomness proposed by McGinnies (1934), Whitford (1949), Blackman (1942), and Fracker and Brischle (1944) were all dependent on quadrat size when the species were actually nonrandom.

It must be kept in mind that while disagreement of these measures with the expected values from the Poisson distribution certainly indicates some kind of nonrandomness of arrangement, agreement does not necessarily imply that the distribution of the plants is random since it is simple to devise non-Poisson distributions such that the measures are the same as those for the Poisson.

The values of $V/\bar{x}$ and K_M, K_F, and K_W in Table V provide these four measures of nonrandomness for the one-meter-quadrat data on the three old-field species under consideration. These measures (and the contagious series results) show that the three species have the following types of distribution:

Index	Most Random to Least Random				
Thomas	Solidago	>	Liatris	>	Lespedeza
Blackman*	Solidago	>	Liatris	>	Lespedeza
McGinnies	Solidago	>	Liatris	>	Lespedeza
Fracker	Solidago	>	Liatris	≥	Lespedeza
Whitford	Solidago	≥	Lespedeza	>	Liatris

* $V/\bar{x}$

The new measure of spacing introduced by Dice (1952) leads to the same conclusion as the measures from the contagious distributions.

These conclusions can be compared with the general appearance of the community as judged by eye from the plots:

Solidago > Liatris > Lespedeza

It is evident that for these species most of these measures arrive at the same conclusion as the visual estimation. The anomalous result from Whitford's index is not surprising in view of its sensitivity to quadrat size (Curtis and McIntosh, 1950). There is also no definite value for complete randomness. This is in sharp contrast to the other measures.

TABLE V
Parameters of the Sampled Plant Populations

	Solidago	Liatris	Lespedeza
Mean $\bar{x}$ or density D	0.06191	0.04188	0.10681
Variance V	0.07640	0.07285	0.29435
Frequency F (per cent)	5.380	3.102	6.047
Abundance $\underline{A}$	1.151	1.350	1.766
Expected density* $\underline{d}$ . .	0.05530	0.03151	0.06238
Measures of randomness†			
Variance/mean $V/\bar{x}$ . .	1.234	1.739	2.756
$K_M = D/d$	1.12	1.33	1.71
$K_F = (D - d)/d^2$	2.16	10.45	11.42
$K_W = 100D/F^2$	0.214	0.435	0.292

* Calculated from the frequency. See Fracker (1944, Table I).

† $V/\bar{x}$ Blackman (1942), etc. Random: $V/\bar{x} = 1$
K_M McGinnies (1934). Random: $K_M = 1$
K_F Fracker (1944). Random: $K_F = 0$
K_W Whitford (1949). Random: K_W is small (0 to 0.3)

SUMMARY

The contagious distributions of Neyman (1939) and Thomas (1949) were fitted to quadrat frequency data on Solidago rigida, Liatris aspera, and Lespedeza capitata in an old-field community. The goodness of fit was excellent, fair, and very bad, respectively. The size of the contagious distribution "clusters" of the mathematical model, 1 to 2 plants per cluster, had little relation to the evident major clumping obvious to the eye, but is more likely related to local clumping effects.

A number of different measures of aggregation or clumping which have been suggested in the literature are discussed. None of these indicates the actual size of the clumps. This seems to be a new problem demanding further research. The relative amount of major clumping of the three species noted by observation was compared with that shown by these different measures and was found to be the same with Lespedeza most clumped, Solidago least clumped, and Liatris in between.

An appendix presents and exemplifies a method for the calculation of the individual terms of the contagious series by means of direct calculation of polynomials instead of by the use of summations.

APPENDIX

Calculation of Terms of Contagious-distribution Series

It is possible that the ecologists who might have tried Neyman's or Thomas' series as a possible mathematical model for quadrat frequency data were deterred by the mathematical complexity of these series. This section shows that it is possible to evaluate the individual calculated terms of these series by the use of simple polynomial functions of variables which can be determined directly from the experimental data. Both series require as starting values the mean and variance of the observed distribution. These are obtained by the usual standard procedures which are described below.

Mean and Variance

Let f be the number of quadrats which contain X plants per quadrat (X = 0, 1, 2, ...), then the mean or average number of plants per quadrat is:

$$\mu_1' = \Sigma(fX)/\Sigma f$$

The summations Σ extend over all the values of X.

The corresponding variance or second moment of the distribution may be most accurately and usually also most easily obtained from the relation:

$$\mu_2 = \frac{\Sigma(fX^2)}{\Sigma f} - \left(\frac{\Sigma(fX)}{\Sigma f}\right)^2$$

As an example consider the data on the distribution of Solidago rigida in the old field (Table VI).

TABLE VI

Calculation of Mean and Variance

Number of Quadrats f	Plants Per Quadrat X	fX	fX²
7229	0	0	0
356	1	356	356
49	2	98	196
5	3	15	45
1	4	4	16
0	>4	0	0
Total 7640		473	613

The summations are:

$$\Sigma f = 7640 \qquad \Sigma fX = 473 \qquad \Sigma fX^2 = 613$$

The mean is:

$$\mu_1' = 473/7640 = 0.061911$$

The variance is:

$$\mu_2 = \frac{613}{7640} - \left(\frac{473}{7640}\right)^2 = 0.076403$$

Neyman's Type A Contagious Distribution

Beall (1939) has shown that calculated values of Neyman's (1939) "Type A Contagious Distribution" can be evaluated by a simple method involving, for each term, the summation of a linear function of the preceding terms of the distribution. This section presents a direct solution such that each calculated value of the series can be obtained from a polynomial in a new variable without the necessity of calculating the preceding terms. The relation was derived by direct substitution in Beall's formulas.

Let m_1 = Neyman's parameter, proportional to the number of "clusters" per quadrat

m_2 = Neyman's parameter, proportional to the number of plants per "cluster"

μ_1' = mean number of plants per quadrat

μ_2 = variance

n_i = calculated number of quadrats each of which contains i plants

n = total number of quadrats, the sum of the n_i

Neyman has shown that m_1 and m_2 may be estimated from the mean μ_1' and variance μ_2 of the observed values by the relations:

$$m_2 = (\mu_2 - \mu_1')/\mu_1'$$

$$m_1 = \mu_1'/m_2 = (\mu_1')^2/(\mu_2 - \mu_1')$$

This is the solution obtained by equating the moments of the theoretical distribution and the moments of the observed distribution. The maximum likelihood solution has been given by Shenton (1949). This method is fairly complicated and requires the moment solution as part of the calculation. Shenton's paper includes a worked out example. Beall's relations for the calculated values are:

$$n_0 = ne^{-m_1(1-e^{-m_2})}$$

$$n_{i+1} = \frac{m_1 m_2 e^{-m_2}}{i+1} \sum_{t=0}^{t=i} \frac{m_2^t}{t!} n_{i-t}$$

The present relations use a new variable, U, which is defined as follows:

$$U \equiv m_1 e^{-m_2}$$

The value of n_1 is:

$$n_1 = m_2 n_0 U$$

The higher terms n_2, n_3, ... are obtained from expressions such as:

$$n_2 = n_1 \frac{m_2}{2!} (1 + U)$$

$$n_3 = n_1 \frac{m_2^2}{3!} (1 + 3U + U^2)$$

$$n_4 = n_1 \frac{m_2^3}{4!} (1 + 7U + 6U^2 + U^3)$$

$$n_5 = n_1 \frac{m_2^4}{5!} (1 + 15U + 25U^2 + 10U^3 + U^4)$$

$$n_6 = n_1 \frac{m_2^5}{6!} (1 + 31U + 90U^2 + 65U^3 + 15U^4 + U^5)$$

that is

$$n_i = n_1 \frac{m_2^{i-1}}{i!} (\text{polynomial in } U^{i-1})$$

The coefficients of the polynomials with the appropriate values of the factorials (i!) are shown in Table VII. The use of these values with a table of powers of m_2 and U permits the direct calculation of any n_i.

Thomas' Double Poisson Series

The double Poisson series of Thomas (1949) is also presented as a summation.

$$n_i = n \sum_{r=1}^{r=i} \frac{m^r e^{-m} (r\lambda)^{i-r} e^{-r\lambda}}{r! \quad (i-r)!}$$

where m = Thomas' parameter, the number of "clusters" per quadrat

λ = Thomas' parameter, one less than the number of plants per "cluster"

n_i = calculated number of quadrats each of which contains i plants

n = total number of quadrats, the sum of the n_i.

This equation may be written in the equivalent form which facilitates the direct calculation:

$$n_i = ne^{-m} \sum_{r=1}^{r=i} \frac{r^{i-r}}{r! \quad (i-r)!} \quad \lambda^{i-r} (me^{-\lambda})^r$$

since the first factor after the summation term is independent of m and λ which must be estimated from the observations. Thomas gives two methods of making this estimation. Method I involves equating the mean μ_1' and variance of the sample to the mean and variance of the distribution. (This is the "moment" solution similar to that used by Neyman for the other series and described above.)

$$\text{Let} \quad g = \mu_2' / \mu_1'$$

$$\text{then} \quad 2\lambda = g - 3 + \sqrt{g^2 - 2g + 5}$$

$$\text{and} \quad m = \mu_1'/(1 + \lambda)$$

Method II, the maximum likelihood estimate, involves only the observed n_0 and n_1:

$$e^{-m} = n_0/n$$

$$e^{-\lambda} = n_1/n_0 m$$

Once m and λ are established the calculated values of n_i can be computed by means of simple polynomials in an analogous manner to the treatment for Neyman's series above. A new variable $V \equiv me^{-\lambda}/\lambda$ is introduced. Direct substitution leads to the following relations:

$$n_0 = ne^{-m}$$

$$\begin{aligned} n_1 &= nme^{-m}e^{-\lambda} \\ &= n_0 \quad \lambda V \end{aligned}$$

$$n_2 = n_1 \frac{\lambda}{2!} (2 + V)$$

$$n_3 = n_1 \frac{\lambda^2}{3!} (3 + 6V + V^2)$$

$$n_4 = n_1 \frac{\lambda^3}{4!} (4 + 24V + 12V^2 + V^3)$$

$$n_5 = n_1 \frac{\lambda^4}{5!} (5 + 80V + 90V^2 + 20V^3 + V^4)$$

$$n_6 = n_1 \frac{\lambda^5}{6!} (6 + 240V + 540V^2 + 240V^3 + 30V^4 + V^5)$$

that is:

$$n_i = \frac{n_1 \lambda^{i-1}}{i!} \text{ (polynomial in } V^{i-1})$$

The coefficients of the polynomials with the appropriate values of the factorials are given in Table VIII. The use of these values with a table of powers of λ and V permits the direct calculation of any n_i, without the necessity of considering the previous terms.

Example: As an example of the use of these polynomials the calculation of the terms in the Neyman's Type A series for the Solidago rigida data is shown below.

$$\mu_1' = 0.061911$$

$$\mu_2 = 0.076403$$

$$m_2 = (0.076403 - 0.061911)/0.061911$$
$$= 0.23408$$

$$m_1 = 0.061911/0.23408 = 0.26449$$

$$e^{-m_2} = 0.79130$$

$$m_1(1 - e^{-m_2}) = (0.26449)(0.20870) = 0.055199$$

$$e^{-m_1(1 - e^{-m_2})} = 0.94630$$

$$n_0 = (7640)(0.96430) = 7229.73$$

$$U = (0.26449)(0.79130) = 0.20929$$

$$n_1 = (0.23408)(7229.73)(0.20929) = 354.19$$

The remaining terms are evaluated using the polynomials. First a table of powers of U and m_2 is prepared:

U	m_2	Factorial
$U = 0.20929$	$m_2 = 0.23408$	2
$U^2 = 0.043802$	$m_2^2 = 0.054793$	6
$U^3 = 0.0091674$	$m_2^3 = 0.012826$	24
$U^4 = 0.0019186$	$m_2^4 = 0.0030023$	720
etc.	etc.	etc.

It is convenient to jot down the appropriate factorial opposite the proper power of m_2 (as has been done above) since it will not only be close to the place where it will be used but also serves to locate the proper polynomial in Table VIII.

The calculation of n_5 serves as an example of the use of the polynomials:

$$\begin{aligned} n_5 &= (354.19)\,(0.0030023/120)\,(1 + (15)\,(0.20929) \\ &\quad + (25)\,(0.043802) + (10)\,(0.0091674) + 0.0019186) \\ &= 0.047 \end{aligned}$$

LITERATURE CITED

ARCHIBALD, E. A. A.

1948 Plant populations. I. A new application of Neyman's contagious distribution. Ann. Bot., 12: 221-35.

ASHBY, E.

1935 The quantitative analysis of vegetation. Ann. Bot., 49: 779-802.

1948 Statistical ecology. II. A reassessment. Bot. Rev., 2: 221-35.

BEALL, G.

1939 Personal communication to J. Neyman. See Neyman (1939, p. 47).

BLACKMAN, G. E.

1935 A study by statistical methods of the distribution of species in grassland associations. Ann. Bot., 49: 749-77.

1942 Statistical and ecological studies on the distribution of species in plant communities. Ann. Bot., 6: 351-66.

CAIN, S. A., and F. C. EVANS

1952 The distribution patterns of three plant species in an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 52.

CLAPHAM, A. R.

1936 Overdispersion in grassland communities and the use of statistical methods of plant ecology. Journ. Ecology, 24: 232-51.

COLE, L. C.

1946 A theory for analyzing contagiously distributed populations. Ecology, 27: 329-41.

CURTIS, J. T., and R. P. McINTOSH

1950 The interrelations of certain analytic and synthetic phytosociological characters. Ecology, 31: 434-55.

DICE, L. R.

1952 Measure of the spacing between individuals within a population. Contrib. Lab. Vert. Biol. Univ. Mich., 55.

EVANS, F. C.

1952 The influence of size of quadrat on the distributional patterns of plant populations. Contrib. Lab. Vert. Biol. Univ. Mich., 54.

EVANS, F. C., and S. A. CAIN

1952 Preliminary studies of the vegetation of an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 51.

FRACKER, S. B., and H. A. BRISCHLE

1944 Measuring the local distribution of Ribes. Ecology, 26: 283-303.

McGINNIES, W. G.

1934 The relation between frequency index and abundance as applied to plant populations in a semiarid region. Ecology, 15: 263-82.

NEYMAN, J.

1939 On a new class of "contagious" distributions, applicable in entomology and bacteriology. Ann. Math. Statis., 10: 35-57.

ROMMEL, L. G.

1930 Comments on Raunkiaer's and similar methods of vegetation analysis and the law of frequency. Ecology, 11: 589-96.

SHENTON, L. R.

1949 On the efficiency of the method of moments and Neyman's Type A distribution. Biometrika, 36: 450-54.

THOMAS, M.

1949 A generalization of Poisson's binomial limit for use in ecology. Biometrika, 36: 18-25.

WHITFORD, P. B.

1949 Distribution of woodland plants in relation to succession and clonal growth. Ecology, 30: 199-208.

Ethyl Corporation, Detroit, Michigan.

Copies of this contribution may be purchased from the University of Michigan
Press, Ann Arbor, Michigan. Price $0.25.

TABLE VII

Coefficients of Powers of U in Polynomials for Neyman's Type A Contagious Distribution

	I	U	U^2	U^3	U^4	U^5	U^6	U^7	U^8	U^9	U^{10}	U^{11}	U^{12}	U^{13}	U^{14}	Factorial
n_2	1	1														2! = 2
n_3	1	3	1													3! = 6
n_4	1	7	6	1												4! = 24
n_5	1	15	25	10	1											5! = 120
n_6	1	31	90	65	15	1										6! = 720
n_7	1	63	301	350	140	21	1									7! = 5 040
n_8	1	127	966	1 701	1 050	266	28	1								8! = 4.0320×10^4
n_9	1	255	3 025	7 770	6 951	2 646	462	36	1							9! = 3.6288×10^5
n_{10}	1	511	9 330	34 105	42 525	22 827	5 880	750	45	1						10! = 3.6288×10^6
n_{11}	1	1 023	28 501	145 750	246 730	179 487	63 987	11 880	1 155	55	1					11! = 3.9917×10^7
n_{12}	1	2 047	86 526	611 501	1 379 400	1 323 652	627 396	159 027	22 275	1 705	66	1				12! = 4.7900×10^8
n_{13}	1	4 095	261 625	2 532 530	7 508 501	9 321 312	5 715 424	1 899 612	359 502	39 325	2 431	78	1			13! = 6.2270×10^9
n_{14}	1	8 191	788 970	10 391 745	40 075 035	63 436 373	49 329 280	20 912 320	5 135 130	752 752	66 066	3 367	91	1		14! = 8.7178×10^{10}
n_{15}	1	16 383	2 375 101	42 355 950	210 766 920	420 693 273	408 741 333	216 627 840	67 128 490	12 662 650	1 479 478	106 470	4 550	105	1	15! = 1.3077×10^{12}

TABLE VIII

Coefficients of Powers of V in Polynomials for Thomas' Double Poisson Distribution

	I	V	V^2	V^3	V^4	V^5	V^6	V^7	V^8	V^9	V^{10}	V^{11}	V^{12}	V^{13}	V^{14}	Factorial
n_2	2	1														2! = 2
n_3	3	6	1													3! = 6
n_4	4	24	12	1												4! = 24
n_5	5	80	90	20	1											5! = 120
n_6	6	240	540	240	30	1										6! = 720
n_7	7	672	2 835	2 240	525	42	1									7! = 5 040
n_8	8	1 792	13 608	17 920	7 000	1 008	56	1								8! = 4.0320×10^4
n_9	9	4 608	61 236	129 024	78 750	18 144	1 764	72	1							9! = 3.6288×10^5
n_{10}	10	11 520	262 440	860 160	787 500	272 160	41 160	2 880	90	1						10! = 3.6288×10^6
n_{11}	11	28 160	1 082 565	5 406 720	7 218 750	3 592 512	792 330	84 480	4 455	110	1					11! = 3.9917×10^7
n_{12}	12	67 584	4 330 260	32 440 320	61 875 000	43 110 144	13 311 144	2 027 520	160 380	6 600	132	1				12! = 4.7900×10^8
n_{13}	13	159 744	16 888 014	187 432 960	502 734 375	480 370 176	201 885 684	42 172 416	4 691 115	286 000	9 438	156	1			13! = 6.2270×10^9
n_{14}	14	372 736	64 481 508	1 049 624 576	3 910 156 250	5 043 886 848	2 826 399 576	787 218 432	118 216 098	10 010 000	484 484	13 104	182	1		14! = 8.7178×10^{10}
n_{15}	15	860 160	241 805 655	5 725 224 960	29 326 171 875	50 438 367 980	37 096 494 435	13 495 173 120	2 659 862 205	300 300 000	19 984 965	786 240	17 745	210	1	15! = 1.3077×10^{12}

CONTRIBUTIONS FROM THE LABORATORY OF
VERTEBRATE BIOLOGY

University of Michigan, Ann Arbor, Michigan

Number 54 March, 1952

THE INFLUENCE OF SIZE OF QUADRAT ON THE DISTRIBUTIONAL PATTERNS OF PLANT POPULATIONS

By FRANCIS C. EVANS

Accepted for publication February 12, 1951

CONTENTS

Introduction 1
Methods 2
Material 3
Results 3
Discussion 10
Summary 13
Literature Cited 14

INTRODUCTION

THE quadrat, a two-dimensional unit of fixed size and shape, generally square but sometimes circular or rectangular, has been one of the principal sampling devices used by ecologists for the past fifty years. From the time of Raunkiaer and Clements, it has been widely employed in gathering quantitative, semiquantitative, or pseudoquantitative information about the structure and organization of plant communities and about the distributional patterns of individual species. The quadrat technique has great practical advantages in field work, for it often requires nothing more than a record of presence or absence, or at most a count of the individuals present. From time to time, however, it has been subjected to considerable criticism. Gleason (1920) seems to have been one of the first to appreciate the fact that the number of individuals likely to be found in a quadrat depended in part upon the size of quadrat employed, and he realized that any statistics resulting from quadrat sampling were influenced accordingly. Since 1920 the shortcomings and imperfections of the quadrat method have become increasingly apparent, and in recent years the ways in which size and number of quadrats affect ecological data have been explored much more precisely. Much of the literature on this subject has been recently reviewed by Curtis and McIntosh (1950). Important additional papers include those of Archibald (1949a, 1949b) and Williams (1950).

A good deal of our knowledge about the effects of quadrat size has been derived from artificially constructed populations (McGinnies, 1934; Penfound, 1945; Curtis and McIntosh, 1950). Opportunity to apply this knowledge to natural populations was provided by a study of three species (Lespedeza capitata, Liatris aspera, and Solidago rigida), components of an old-field grassland community on the Edwin S. George Reserve, of the University of Michigan, Livingston County, southeastern Michigan. A preliminary description of this community has recently been published (Evans and Cain, 1952), and the positions of individual plants of these three species as they occurred on an area of approximately two acres within the community have been mapped and charted (Cain and Evans, 1952). For each of these populations, the frequency data obtained by using a quadrat size of one square meter have been subjected to analysis from the standpoint of "contagious" distribution functions by Thomson (1952). In the present paper these populations have been re-examined by employing quadrats of several sizes, and a comparison of the results is provided as a demonstration of the influence of quadrat size on distributional data.

Acknowledgments

I should like to thank William B. McIntosh and William Prychodko for assistance in making the statistical computations, and Lee R. Dice and George W. Thomson for helpful advice in the preparation of this manuscript. The author accepts responsibility for any errors present.

METHODS

The map prepared by Cain and Evans (1952) was subdivided into quadrats, each of which was four meters square. This yielded a total of 429 quadrats lying completely within the boundaries of the mapped populations and covering an area of 6864 square meters. These quadrats were then further subdivided into a series of increasingly smaller units, each subdivision doubling the number of quadrats and halving their size. The full series consisted of the following quadrat sizes: 16, 8, 4, 2, 1, 1/2, 1/4, 1/8, and 1/16 square meters, respectively.

The number of individual plants occurring in each quadrat of each size was recorded for all three species under study. All quadrats of each size were examined, so that the total area and the total population remained constant for the entire series. Differences in the results for the different quadrat sizes are, therefore, not due to errors of random sampling.

MATERIAL

Within the 6864 square meters covered by this study, there were 696 Lespedeza, 388 Solidago, and 298 Liatris plants, respectively. Calculated values of density (number of plants per square meter) are as follows: Lespedeza, 0.1014; Solidago, 0.0565; and Liatris, 0.0434. Thus, these populations displayed a low order of density — very much lower, for example, than that exhibited by the two dominant grasses of the community, Poa compressa and Aristida purpurascens, each of which exceeded 500 culms per square meter (Evans and Cain, 1952). These density values do not represent minimal ones in this community, however, for they are considerably higher than those shown by such species as Lactuca pulchella, Tragopogon pratensis, and Lithospermum croceum. They are, in fact, quite typical of the sort of values the field ecologist frequently encounters.

On the basis of frequency (per cent of the total number of quadrats which represent occupied ones) data obtained from meter-square quadrats, Thomson (1952) has pointed out that the distributions of all of these populations depart radically from expectation for randomly distributed values. The comparison of data from such strongly skewed populations presents considerable difficulty, but it must again be emphasized that biologists are commonly faced with material of this sort.

RESULTS

Relation of Density to Quadrat Size

When expressed as the number of individuals per unit of area, density values obviously remain constant regardless of quadrat size. If density is defined as the number of individuals per quadrat, however, it is clear that density becomes directly proportional to quadrat size, doubling in value with each two-fold increase of quadrat area (Table I). In either case, two or more species will maintain similar density relationships for every quadrat size. As indicated above, the three species here examined may be listed in order of decreasing density as follows: Lespedeza, Solidago, and Liatris.

Relation of Frequency to Quadrat Size

The same relationships do not hold for frequency values for these species (Table I). In no case is there a constant doubling of frequency with doubling of quadrat size; in fact, the rate of increase in frequency lessens with each increase in size of quadrat. The frequency relationships among the three species also change as the quadrat size changes. Solidago, for example, which is only slightly more frequent than Liatris and roughly half as frequent as Lespedeza in the smallest quadrats, is twice as frequent as Liatris and one-and-one-half times as frequent as Lespedeza in the largest quadrats. Estimates of relative frequency, then, are affected by the size of quadrat employed.

TABLE I.

Relation Of Density (Number of Plants Per Quadrat Examined), Frequency (Per Cent of Quadrats Occupied), and Abundance (Number of Plants Per Occupied Quadrat) to Quadrat Size for Three Component Species of an Old-Field Community, Edwin S. George Reserve, Livingston County, Michigan

Quadrat Size (sq. m.)	Number of Quadrats	Number of occupied quadrats			Density			Frequency			Abundance		
		Lespedeza	Liatris	Solidago	Lespedeza	Liatris	Solidago	Lespedeza	Liatris	Solidago	Lespedeza	Liatris	Solidago
0.0625	109,824	658	292	386	0.0063	0.0027	0.0035	0.60	0.27	0.35	1.06	1.02	1.01
0.125	54,912	626	285	382	0.0127	0.0054	0.0071	1.14	0.52	0.70	1.11	1.05	1.02
0.25	27,456	566	274	378	0.0254	0.0109	0.0141	2.06	1.00	1.38	1.23	1.09	1.03
0.5	13,728	497	253	366	0.0507	0.0217	0.0283	3.62	1.84	2.67	1.40	1.18	1.07
1.	6,864	401	221	340	0.1014	0.0434	0.0565	5.84	3.22	4.95	1.74	1.35	1.14
2.	3,432	308	185	318	0.2028	0.0868	0.1131	8.97	5.39	9.27	2.26	1.61	1.22
4.	1,716	224	152	291	0.4056	0.1737	0.2261	13.05	8.86	16.96	3.12	1.96	1.33
8.	858	170	124	243	0.8111	0.3473	0.4522	19.81	14.45	28.32	4.09	2.40	1.60
16.	429	120	92	184	1.6224	0.6947	0.9044	27.97	21.45	42.89	5.80	3.24	2.11

Relation of Abundance to Quadrat Size

Abundance is here defined as the number of individuals per occupied quadrat. Values of abundance for Lespedeza, Liatris, and Solidago are also shown in Table I. Although these species retain the same order of relative abundance throughout the series of quadrat sizes, the differences among the abundance values become greater with increased quadrat size, but not proportionally so. This is clearly to be expected when the species being compared have distribution patterns showing different degrees of clumping. Curtis and McIntosh (1950) point out that abundance is derived from both density and frequency, having the following relationship to them: abundance = 100 x density/frequency, where frequency is a percentage and density is the number of individuals per quadrat. It should be noted that for the smallest quadrat size (0.0625 square meters) the three species are almost equally abundant, each approaching the minimal value of 1.00. Thus the size of quadrat employed may determine one's estimate of relative abundance.

Relation of Frequency Distribution to Quadrat Size

Table II indicates the changes in frequency distribution which appear when the size of quadrat is altered. The most obvious result of increasing quadrat size is a lengthening of the tail of the distribution. The larger the quadrat, the more likely it is to contain many individuals and the less likely it is to have none. As more and more of the individuals present are found together in the larger quadrats, the number of quadrats containing only one individual decreases with each larger quadrat size, but, due to the reduction in total number of quadrats, the absolute frequency with which this class occurs actually increases. Quadrats with two or three individuals show a gradual increase in numbers up to a certain quadrat size, beyond which they decline. Some indication of the differences in degree of clumping shown by these species is seen in the data for the largest quadrats; as many as 63 Lespedeza plants were recorded in a single 16-square-meter quadrat, where the number of Solidago present never exceeded 14.

The data for each quadrat size have been fitted to a Poisson series, using the chi-square test for comparison with the values expected for randomly distributed populations. The chi-squares for Lespedeza and Liatris indicate highly significant departures from expectation for all quadrat sizes. This is true also for Solidago with the exception of the chi-square for the smallest quadrat size, which does not show any significant difference between the observed and the expected distribution. In this latter case, the size of the quadrat has been so reduced that the occurrence of more than one individual per quadrat is an extremely rare event. Preston (1948) has made the point that, for the Poisson distribution laws to apply, there must be room in the quadrat for more individuals than actually occur. The data in Table II suggest that a quadrat 1/16 of a square meter in area approaches the lower limits of space required by individual plants of these three species under present conditions within the community.

TABLE II

Relation of Frequency Distribution to Quadrat Size for Three Component Species of an Old-field Community, Edwin S. George Reserve, Livingston County, Michigan

Plants Per Quadrat	Quadrat Size in Square Meters								
	0.0625	0.1250	0.2500	0.5000	1.0000	2.0000	4.0000	8.0000	16.0000
	Lespedeza								
0	109,166	54,286	26,890	13,231	6,463	3,124	1,492	688	309
1	622	566	465	362	250	164	98	68	44
2	34	50	83	98	80	58	42	24	15
3	2	10	11	24	37	30	29	21	12
4	0	0	4	5	14	19	13	11	6
5			2	3	11	11	6	6	6
6			1	4	3	12	7	8	4
7			0	1	4	5	6	8	2
8				0	1	2	4	0	3
9					0	4	5	4	1
10					1	2	3	3	4
11					0	0	3	5	2
12						0	3	3	2
13						0	0	2	2
14						0	1	2	2
15						0	2	1	2
16						1	0	1	5
17						0	0	0	2
18							0	0	1
19							1	0	2
20							0	0	0
21							0	0	1
22							1	0	0
23							0	0	0
29								1	0
34								2	0
37								0	1
63									1
64 or more									0
Chi-square	498.4	704.2	938.0	955.4	661.2	460.7	769.6	813.8	918.6

TABLE II (Cont.)

Plants Per Quadrat	Quadrat Size in Square Meters								
	0.0625	0.1250	0.2500	0.5000	1.0000	2.0000	4.0000	8.0000	16.0000
					Liatris				
0	109,532	54.627	27,182	13,475	6.643	3.247	1.564	734	337
1	286	272	252	218	169	125	92	68	40
2	6	13	20	28	37	34	28	20	19
3	0	0	2	5	9	16	19	16	6
4			0	1	3	3	4	9	7
5				1	2	3	3	4	9
6				0	1	1	1	1	4
7					0	1	1	1	1
8						1	0	0	3
9						1	0	2	0
10						0	2	0	1
11							1	0	0
12							1	1	0
21							0	1	1
22								1	0
43								0	1
44 or more									0
Chi-square	15.5	173.4	139.1	340.7	379.7	270.7	169.6	342.9	194.8
					Solidago				
0	109,438	54,530	27,078	13,362	6.524	3.114	1.425	615	245
1	384	376	368	344	295	258	222	162	94
2	2	6	10	22	42	52	51	48	36
3	0	0	0	0	3	6	13	20	31
4					0	2	2	5	8
5						0	2	4	10
6							0	1	0
7							1	1	2
8							0	1	0
9								1	1
10								0	1
14									1
15 or more									0
Chi-square	3.66	15.3	20.4	55.1	126.9	100.9	52.9	97.9	107.9

The Poisson series evidently does not provide a basis for an adequate representation of these contagiously distributed species. Thomson (1952) found it necessary to use a more complex distribution function for the treatment of the data obtained from the one-square-meter quadrats. Similar considerations evidently obtain for the other quadrat sizes.

Relation of Measure of Dispersion to Quadrat Size

One of the most important features of any distributional pattern is the degree to which it departs from random expectation. To measure this dispersion, a number of ecologists, including Blackman (1942), have made use of the well-known fact that in the Poisson series the variance is equal to the mean. This measure assumes that the extent to which the variance:mean ratio deviates from unity will express the departure from randomness, and, vice versa, that the more nearly it approaches a value of 1.00 the greater the conformity to a random distribution. Other workers have tried to exploit the relationship that exists between frequency and density in a randomly distributed population. This relationship can be expressed by the formula

$$F = 100\,(1 - e^{-D})$$

where F is frequency, D is density and e is the base of the natural or Napierian logarithms (Curtis and McIntosh, 1950). For random distributions, then, it is possible to calculate density values for any known level of frequency. McGinnies (1934) used this fact to obtain the ratio between the observed density and the density calculated from frequency values. Here also departure from unity is taken to indicate degree of nonrandomness. Fracker and Brischle (1944) modified this measure by taking the ratio of the difference between observed and expected densities to the square of the expected density. Whitford (1949) employed the ratio of abundance to frequency, or, since abundance is equal to the density divided by the frequency index, the ratio of the density to the square of the frequency. The effects of quadrat size upon each of these four measures of dispersion have been considered by Curtis and McIntosh (1950) with examples drawn from artificially constructed random, regular, and contagious population distributions. When their populations were clumped, all of these measures proved to be dependent upon quadrat size, and Whitford's measure was shown to be so sensitive that its use is not recommended for species whose density is such as to give frequencies of less than 20 per cent.

Table III gives the values of these four measures of dispersion for the Lespedeza, Liatris, and Solidago populations as calculated for each size of quadrat. For Blackman's and McGinnies' measures, in which a value greater than unity is said to indicate a tendency to clumping, the effect of quadrat size is readily observed; the difference between successive values is not directly proportional to size of quadrat but becomes greater with each increase of quadrat size. It should be noted that the values of both of these measures for the smallest-sized quadrats used in this study, approach the theoretical value of 1, expected for a random

TABLE III

Effects of Quadrat Size on Various Measures of Dispersion for Three Component Species in an Old-field Community, Edwin S. George Reserve, Livingston County, Michigan

V = variance, $\bar{x}$ = mean density, D = actual density, d = expected density, F = frequency.

Quadrat Size (sq.m.)	Blackman (1942) $V/\bar{x}$			McGinnies (1934) D/d			Whitford (1949) $100D/F^2$			Fracker and Brischle (1944) $(D-d)/d^2$		
	Lespedeza	Liatris	Solidago	Lespedeza	Liatris	Solidago	Lespedeza	Liatris	Solidago	Lespedeza	Liatris	Solidago
0.0625	1.102	1.038	1.007	1.0289	1.0192	1.0028	1.7657	3.8373	2.8595	4.6916	7.1983	0.8025
0.125	1.217	1.082	1.024	1.1055	1.0429	1.0122	0.9753	2.0205	1.4599	9.2085	8.2349	1.7439
0.25	1.478	1.164	1.038	1.2171	1.0822	1.0195	0.5965	1.0900	0.7700	10.4207	8.1909	1.4063
0.5	1.843	1.341	1.085	1.3749	1.1669	1.0441	0.3868	0.6391	0.3976	10.1655	8.9697	1.6278
1.	2.586	1.742	1.206	1.0845	1.3266	1.1127	0.2971	0.4188	0.2304	11.3707	9.9792	2.2181
2.	3.864	2.424	1.310	2.1568	1.5670	1.1627	0.2518	0.2988	0.1317	12.3024	10.2013	1.6735
4.	6.319	3.399	1.512	2.8996	1.8724	1.2168	0.2380	0.2213	0.0786	13.5805	9.4062	1.1666
8.	9.809	5.874	1.983	3.6736	2.2251	1.3581	0.2066	0.1663	0.0564	14.1589	7.8483	1.0754
16.	15.319	12.193	2.633	4.9445	2.8779	1.6145	0.2074	0.1510	0.0492	12.0218	7.7799	1.4156

distribution, whereas it has already been demonstrated that these populations are not randomly distributed. Furthermore, the values for the three species are very nearly alike at this lower level, apparently indicating little difference among them. If, then, the data for the smallest quadrats had been the only material available, these measures would give a false impression of the situation.

The values for Whitford's index also show a clear-cut relationship to quadrat size, and their range is indicative of the sensitivity of the measure to this factor. In other respects, Whitford's measure differs from those of Blackman and McGinnies, for it shows its greatest percentage differences between successive values at the smallest quadrat sizes. Since, in this measure, the lower the value the closer the approximation to a random distribution, these data seem to suggest that the smallest-sized quadrats indicate a greater departure from randomness than do the quadrats of larger size, which is just the reverse of the picture obtained from the measures of McGinnies and Blackman. If the three species are compared on the basis of Whitford's measure, their relative positions are found to shift as the quadrat size is altered; this is expected because this measure makes use of frequency values, and differences in relative frequency have already been indicated (Table I.). For the four smaller quadrat sizes (1/16, 1/8, 1/4, and 1/2 square meters) Lespedeza is rated most random, Solidago next, and Liatris least; for the 1- and 2-square-meter quadrats, Solidago is most random, Lespedeza next, and Liatris least; and for the three larger quadrats (4, 8, and 16 square meters), Solidago is most random, Liatris next, and Lespedeza least.

Fracker and Brischle's measure proved unique in not exhibiting any definite relationship to size of quadrat, although the values were clearly affected by it. This measure, like that of Whitford, approaches zero for random distributions. It gives the greatest degree of differentiation among the three species at any given quadrat size. Its values agree with those of Blackman's and McGinnies' measures in assigning the most nearly random distribution to Solidago, but the three species do not maintain similar relationships throughout the series, for Lespedeza shifts from an intermediate position for the smallest quadrat size to the least randomly distributed for all larger-sized quadrats.

All of these measures are clearly influenced by the size of the quadrat used to obtain the basic data. It seems likely that disagreement in the results of various authors stems in part from differences in the sizes of their quadrats, and that success or failure in the application of these measures depends upon a fortunate or unfortunate choice of quadrat size.

DISCUSSION

As noted above, the smallest-sized quadrats yielded values for Blackman's measure involving the ratio of the variance to the mean which closely approximate unity, as expected for randomly distributed populations. A hypothetical example will be given to show that a distribution may depart radically from that of a Poisson series and still have a variance exactly equal to the mean. If 101 individuals are distributed in 101 quadrats in such a way that 37 quadrats contain 0 individuals, 38 contain 1, 18 contain 2, 6 contain 3, 1 contains 4, and 1 contains 5, both the mean density and the variance will be found to equal 1.00, and a chi-square test gives a value of 0.036 (d.f. = 1), which does not indicate any significant difference from a Poisson distribution. However, if these same 101 individuals are distributed among the same 101 quadrats in such a way that 20 quadrats contain 0 individuals; 76 contain 1; and 5 contain 5, the variance is still equal to the mean density, that is, 1.00, but a chi-square test gives a value of 75.17 (d.f. = 1), indicating a highly significant departure from a Poisson distribution. Thus, as Thomson (1952) has pointed out, disagreement of observed values with those expected for the Poisson distribution certainly indicates some kind of nonrandom arrangement, but agreement by no means necessarily implies that the observed distribution is a random one. Measures which employ the ratio of the variance to the mean as a coefficient of dispersion are therefore not completely reliable.

Measures of dispersion which are based on the relation between density and frequency in a randomly distributed population are also open to objections. This relation does not fully describe the population distribution; it considers only the over-all mean density and the zero class of the frequency distribution. An adequate distribution description should take into account the form or shape of the distribution curve, and the contributions to the departure from randomness that may be made by classes other than the zero class. In contagiously distributed populations some one class may contribute a major part of the total dispersion. For example, in the frequency distribution for the Liatris data obtained from the smallest-sized quadrats (Table II), the class containing two individuals per quadrat contributed almost all of the departure from randomness (15.1 out of the total chi-square of 15.5). I have already indicated the effect that quadrat size may have upon the frequencies with which contagiously distributed populations occur in quadrats. Any evaluation of dispersion which is based on frequency will therefore be influenced by the size of quadrat used in obtaining the frequency values.

Similar criticism appears to be equally applicable to measures based in part upon the density calculated from frequency values, for this calculated density is really that which is expected for a random distribution. If the frequency is very low, of the order of 0.10 or less, the frequency-density relationship expressed by the formula given above is closely approximated for contagious distributions, provided that the quadrat size is such as to make the occurrence of more than one individual per quadrat a rare event. Where greater frequencies occur, however, or if quadrats including several to many individuals are often encountered, contagiously distributed populations do not exhibit the expected relationship between density and frequency, and it becomes impossible to calculate one from the other.

In sampling plant populations in the field, ecologists have ordinarily employed only one quadrat size in any given investigation. The above demonstration of the different results obtained with large and small quadrats, however, indicates a source of considerable error in the one-quadrat approach and suggests the desirability of utilizing several sizes of quadrat in securing samples for the study of distribution patterns and other phytosociological characters. The extra time and labor involved is not excessive, and the additional information obtained is well worth the cost. With material obtained by quadrats of several sizes, it is possible to put the frequency-density relationship to practical use. With randomly distributed populations, if frequency is plotted against density for each quadrat size, the points will be found to lie on a characteristic curve (Fig. 1). Corresponding data for any nonrandom population may be plotted in similar fashion, and the resulting curve can be compared with the one for the theoretical random distribution. This has been done in Figure 1 for the observed populations of Lespedeza, Liatris, and

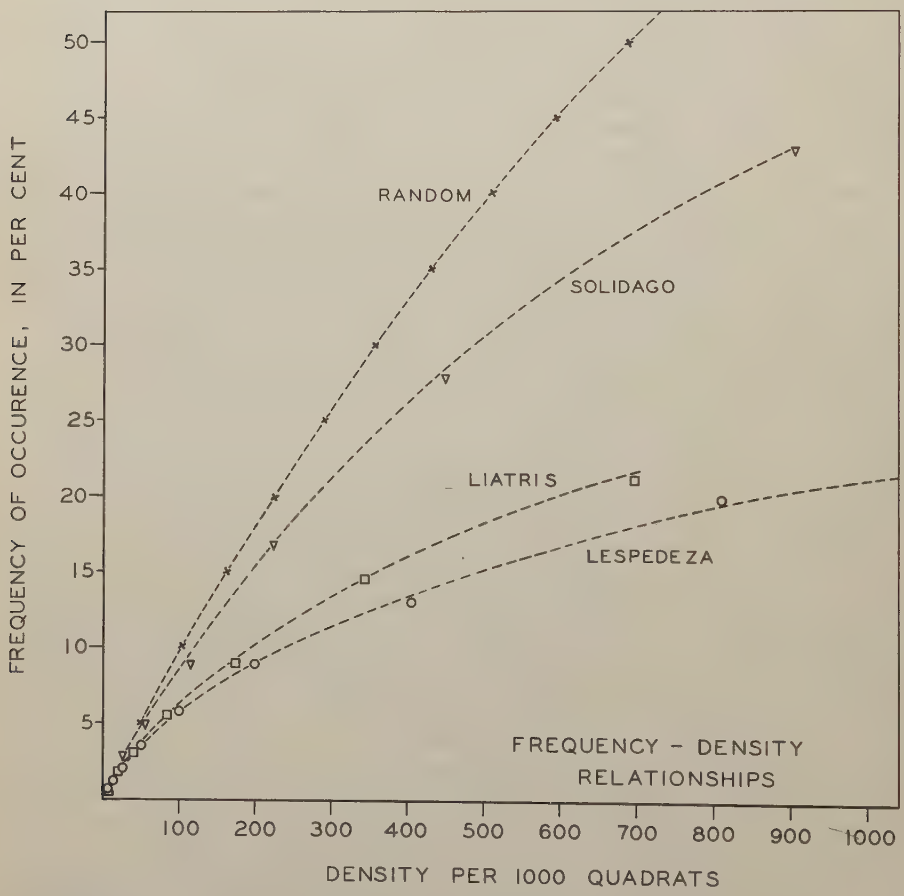


FIG. 1. Frequency-density relationships for a random distribution and for populations of three component species of an old-field community, Edwin S. George Reserve, Livingston County, Michigan.

Solidago. The tendency to contagious distribution is shown by a flattening of the theoretical curve, while departure from randomness in the opposite direction, that is, towards greater regularity of occurrence, would be indicated by a curve steeper than that for the random distribution. Each of the observed populations evidently departs markedly from randomness, with Solidago displaying the greatest degree of conformity to a random distribution, and Lespedeza the least. This is in harmony with the estimation of relative clumping observable in the field or by inspection of the mapped distribution patterns, but the divergence of the curves gives a clearer picture of the degree to which these populations depart from randomness. Similar curves were derived by Curtis and McIntosh (1950) in sampling artificial populations, and there is good agreement here between their theoretical data and those obtained from field studies.

In conclusion then, values of many phytosociological characteristics which are estimated from a single quadrat size may give an erroneous impression, especially if the species concerned are strongly clumped. If quadrats of several sizes are employed in collecting data, the frequency-density curve that can be derived will enable one to determine, qualitatively at least, the degree to which the observed distributions depart from randomness and by extrapolation or interpolation to compare two or more sets of data obtained with quadrats of different size.

SUMMARY

The distributional patterns of populations of Lespedeza capitata, Liatris aspera, and Solidago rigida occurring in an old-field grassland community in southeastern Michigan have been subjected to analysis by quadrats of several different sizes. The size of quadrat was found to affect the resulting values of frequency and abundance, as well as the frequency distributions of the number of individuals per quadrat. It was also shown to have a marked effect upon various measures of dispersion. This demonstration suggests the desirability of utilizing several sizes of quadrat in securing samples for the study of distribution patterns and other phytosociological characteristics. If data for several quadrat sizes are available, a frequency-density curve may be derived that will enable one to determine qualitatively the degree to which the observed distributions depart from randomness and to compare material obtained with quadrats of different size.

LITERATURE CITED

ARCHIBALD, E. A. A.

1949a The specific character of plant communities. I. Herbaceous communities. Journ. Ecol., 37: 260-73.

1949b The specific character of plant communities. II. A quantitative approach. Journ. Ecol., 37: 274-88.

BLACKMAN, G. E.

1942 Statistical and ecological studies on the distribution of species in plant communities. Ann. Bot., 6: 351-66.

CAIN, S. A., and F. C. EVANS

1952 The distribution patterns of three plant species in an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 52.

CURTIS, J. T., and R. P. McINTOSH

1950 The interrelations of certain analytic and synthetic phytosociological characters. Ecology, 31: 434-55.

EVANS, F. C., and S. A. CAIN

1952 Preliminary studies of the vegetation of an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 51.

FRACKER, S. B., and H. A. BRISCHLE

1944 Measuring the local distribution of Ribes. Ecology, 25: 283-303.

GLEASON, H. A.

1920 Some applications of the quadrat method. Bull. Torrey Bot. Club, 47: 21-33.

McGINNIES, W. G.

1934 The relation between frequency index and abundance as applied to plant populations in a semi-arid region. Ecology, 15: 263-82.

PENFOUND, W. T.

1945 A study of phytosociological relationships by means of aggregations of of colored cards. Ecology, 26: 38-57.

PRESTON, F. W.

1948 The commonness, and rarity, of species. Ecology, 29: 254-83.

THOMSON, G. W.

1952 Measures of plant aggregation based on contagious distributions. Contrib. Lab. Vert. Biol. Univ. Mich., 53.

WHITFORD, P. B.

1949 Distribution of woodland plants in relation to succession and clonal growth. Ecology, 30: 199-208.

WILLIAMS, C. B.

1950 The application of the logarithmic series to the frequency of occurrence of plant species in quadrats. Journ. Ecol., 38: 107-38.

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price $0.25.

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

University of Michigan, Ann Arbor, Michigan

Number 55 March, 1952

MEASURE OF THE SPACING BETWEEN INDIVIDUALS WITHIN A POPULATION

By LEE R. DICE

Accepted for publication May 11, 1951

CONTENTS

Introduction 1
Method for Measuring Spacing Between Individuals 3
Statistical Treatment of Measurements of Spacing 7
Relation of Type of Distribution to Spacing between Individuals 7
Comparison of Spacing in Different Populations 16
Relationship Between Spacing and Population Density 17
Spacing as a Measure of Association Between Species 18
Summary 21
Literature Cited 22

INTRODUCTION

SPACING in nature between individual organisms of a given species is of great ecologic significance. The tendency of individuals to occur singly or in aggregations affects the degree of utilization of the local habitat. The spacing of the individuals within a community, furthermore, affects all those social or ecologic interrelations that may exist at any given time among the individuals of the same or of differing species. Methods for describing accurately the spacing of the individuals are consequently needed in any consideration of the organization either of societies or of communities.

Methods for measuring the spacing between individual plants have been proposed by several ecologists (Raunkiaer, 1934; Cottam and Curtis, 1949). Unfortunately, none of the proposed methods provides for the statistical treatment of the measurements, and they have other deficiencies as well.

Since a practical method for the direct measure of the spacing between the individuals making up a population is lacking, their pattern of distribution has in the past been deduced mostly from counts of the number of individuals on sample plots taken at random. If the individuals are distributed over an area at random, the number of sample plots containing 0, 1, 2, 3, and so on, individuals should fall into a Poisson series. Inasmuch as the variance of a Poisson series is equal to the mean of the series, a comparison between the variance and the mean of the samples gives information about the type of distribution of the individuals. A variance that is less than the mean indicates a spacing of individuals that is more uniform than random, while a variance that is larger than the mean indicates a tendency of the individuals to occur in clumps or groups (Fisher, 1915; Beall, 1935; Clapham, 1936).

The variance/mean ratio gives a rough indication of whether or not the distribution of a species in a particular series of samples is random, but no satisfactory mathematical procedure is available for measuring the significance of the divergence of any particular variance/mean ratio from that expected in a random distribution, nor for comparing the differences between the distribution patterns of two or more series of samples (Cole, 1946). A large number of plots must be sampled in order to secure a reliable basis for calculation. The results also are seriously affected by the population densities and by the sizes of the sample plots employed (Evans, 1952). Furthermore and of utmost importance, no direct measure is obtained by the sample-plot method of the actual distances between the individuals.

In order to overcome these difficulties I have for several years been experimenting with methods for measuring directly the spacing of the individuals in a community. In the following sections I shall describe the method that has proved most efficient for this purpose and shall present several examples of its application to concrete cases.

The populations of plants whose spacing is here described are on the Edwin S. George Reserve of the University of Michigan, Livingston County, Michigan (Evans and Cain, 1952). Measurements of the spacing of three of the species, Solidago rigida (goldenrod), Lespedeza capitata (bush clover), and Liatris aspera (blazing star), have been made on a large chart constructed by Cain and Evans (1952) of the distribution of these plants over a grassy plot covering 7873 square meters. The spacing of Hieracium longipilum (hawkweed) was measured directly in the field on a grassy plot covering 267 square meters. The spacing of the forest trees was also measured in the field on a plot covering 6856 square meters.

Acknowledgments

For assistance in taking measurements in the field of the spacing between individual plants I am indebted to Elizabeth Dice, Francis C. Evans, and John A. King. Stanley A. Cain and Francis C. Evans (1952) have kindly allowed the use of their large chart on which the distribution of three species of plants had been plotted. Measurements of the distances between the plants on this chart were made by William B. McIntosh and William Prychodko, who also made most of the statistical computations here presented. John A. King made the plot of random dots used in a part of the study. George W. Thomson has given valuable advice on statistical methods.

METHOD FOR MEASURING SPACING BETWEEN INDIVIDUALS

In order to obtain a basis for the calculation of means and of the variability of spacing between individuals within populations it is necessary to adopt a standard procedure for taking the measurements. After a considerable amount of experiment with various procedures, I propose the following method:

1. The necessary number of individuals to be taken as points of origin for the measurements are located by some process of random sampling.
2. From the center of each individual which is taken as a point of origin the distance is measured to the nearest other individual of the same kind in each of the 6 surrounding sextants (Fig. 1). From each point of origin 6 independent measurements of spacing are consequently obtained.

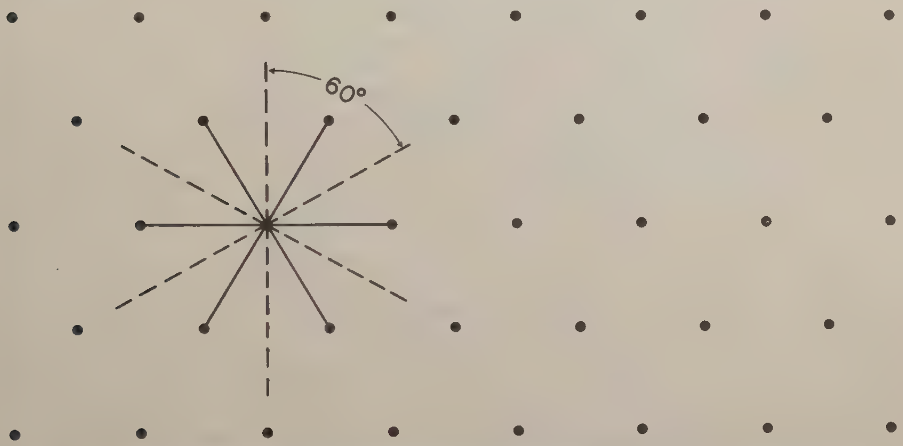


FIG. 1. Method proposed for measurement of spacing between individuals which are evenly spaced over a plane surface. From any individual taken as a point of origin, the distance is measured to the nearest adjacent individual in each of the surrounding sextants (marked by broken lines).

3. The measurements of the distances between individuals obtained by this procedure may then be treated by the statistical methods to be described in a later section of this paper.

Instruments

For laying out the sextants around each point of origin a surveyor's transit or a sighting compass may be used. One procedure is to set a compass on a tripod centered exactly over the individual which forms the point of origin. Assume that a magnetic south-north line forms the western boundary of the first sextant. Now rotate the sights 60 degrees clockwise to locate the other boundary of this first sextant. Measurement is then made with a steel tape or rule to the nearest adjacent individual within this sextant. The compass sights are then rotated another 60 degrees further clockwise to delimit the next sextant, and so on.

A special instrument with 6 equally spaced arms radiating outward from a common center greatly facilitates the taking of the measurements. The space between any 2 arms forms a sextant. The device which I have constructed (Fig. 2) is made of heavy brass and has sufficient weight not to be easily displaced while the measurements are being made. The center of the instrument is placed directly over the individual chosen to be the center of origin for the measurements. The instrument may either be placed directly on the ground, in which case it will crush any delicate plant somewhat, or it may be supported on a tripod. A magnetic compass is used to orient 1 arm of the instrument to point north. One end of a steel tape is next fastened to the center pin of the instrument, so that its zero reading is exactly in the center of measurement. A single observer can now locate the sextants by sighting along the arms and also can measure directly the distance to the nearest plant in each sextant. An assistant to record the measurements as they are taken, however, will expedite the field work.

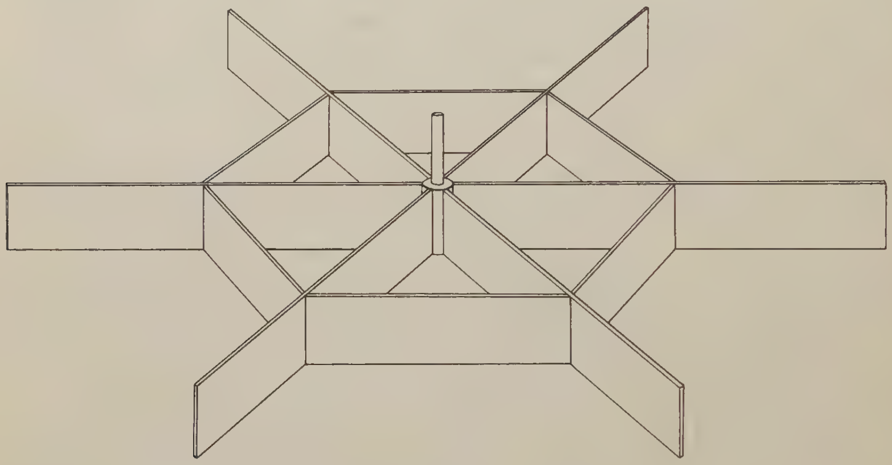


FIG. 2. Instrument devised for delimiting the sextants surrounding a point of origin. To a central cylinder of brass 3/4 inch in diameter, 6 equally spaced arms are soldered. Each arm is made of a strip of brass 1/8 by 1-1/2 by 12 inches. Braces between the arms midway of their lengths enforce rigidity for the device. The central cylinder is tapped above to receive a 1/4-inch brass pin and below to receive a camera-tripod screw.

Random Sampling

For selecting the individual organisms which are to be used as centers of origin for the measurements of spacing, some method of random sampling must be used. If the total number of individual organisms on the plot to be sampled is not very great, each of them may be numbered serially. Small cardboard price tags, each with a string attached, are satisfactory for this purpose. Before going into the field the tags should be numbered serially and placed in order on a wire loop. From a table of random numbers the points of origin are then drawn. If, for example, approximately 300 measurements are desired, then 50 points of origin may be drawn.

A less laborious method is to begin at 1 edge of the plot to be covered and as each individual organism is encountered to make a random drawing to ascertain whether or not this individual is to be taken as a point of origin for the measurements. If a preliminary survey should indicate, for example, that about one-tenth of the individuals should be taken as points of origin in order to obtain the desired number of measurements, then by drawing a card from a set numbered from 1 to 10 as each individual is encountered, one would measure from that individual only if the card drawn was, say, a 9. The individuals can be marked as they are encountered by attaching a wisp of cotton, by splashing them with a dash of talcum powder, or in some other simple manner.

Still another method of random sampling is to run several line transects through the area at locations selected at random and to take as the points of origin the nearest individuals to points taken at random along the transects. A somewhat similar method has been suggested by Cottam and Curtis (1949), but it is not fully random.

Difficulties Sometimes Encountered

Sometimes it is difficult to locate the precise middle of an individual which is to serve as a point of origin or as an end point for the measurements of spacing. For most plants it will be best to take as the point of measurement the middle of the main stem where this emerges from the ground. If there is no main stem, but instead only a group of stems, then the middle point among the stems will serve as the point of measurement.

It will be impossible to measure the spacing of active mobile animals, except as these may be located at some fixed instant of time, as might be true if they were photographed from above. In such case the point of origin of the measurements could either be taken to be the middle of the main part of the body or of the head. So long as the method of taking the measurement is clearly stated and the observer is consistent in his procedure, it should make little difference what point of origin is taken. For those sessile animals which lack a clearly defined head, the middle of the body can be taken as the point of origin for the measurements.

Where the point of origin is a tree or bush over which the sighting compass or other instrument cannot be set up, the position of the compass used to locate the sextants can be shifted a specified distance to the right or to the left. Allowance for this shift must then be made when ascertaining which is the nearest other individual in each sextant, always keeping in mind that the sextant under consideration surrounds the actual point of origin and not the shifted position occupied by the compass. The actual measurements of spacing will of course be made directly from the point of origin to the nearest individual in each sextant.

Frequently, when taking measurements of spacing, no individual of the appropriate kind is encountered within a particular sextant until the boundary of the plot under study is reached. If the plot is surrounded by habitat of essentially the same character as that within the plot, then I see no objection to measuring to the nearest individual within the sextant concerned, irrespective of whether that individual is inside or outside of the artificial boundaries of the plot. On the other hand, if the type of habitat changes, either within or outside the plot, in a way that might affect the distribution of the individuals in a particular sextant, then that sextant should be omitted from consideration. It may consequently happen that fewer than 6 measurements of spacing may be obtained from some points of origin.

The reduction in number of measurements from any point of origin below 6, by reason of failure of occurrence of any individual of the species under consideration in the sextant concerned until the boundary of the plot is reached, will tend to depress the calculated mean of the spacing between individuals. This is true because the omission usually will indicate a more than average gap between individuals in that direction. One should consequently strive to avoid such incomplete measurements. One way to accomplish this is to omit as points of origin any individuals which happen to lie closer to a boundary of the plot than some previously chosen distance, say about twice the expected mean distance between individuals.

Should 2 points of origin lie close together, it may happen that the distance between these 2 individuals will be represented in 2 sets of sextant measurements. Inasmuch as such duplicated measurements will occur most frequently between closely adjacent individuals, the inclusion of duplicate measurements in the calculation of a mean will tend toward an erroneous lowering of its value. Only 1 measurement between any 2 points should consequently be included in the calculations and all duplicate measurements should be discarded.

Items to be Treated as Individuals

In the measurement of the spacing in any population, careful definition must be made of the items which are to be treated as individuals. It must be clearly stated, for example, whether all individuals of a given species, irrespective of size, sex, or age class, have been considered or whether the spacing between individuals belonging only to certain classes has been measured. Individuals belonging to different species can be considered to be members of the same population for the purpose of measuring their spacing. For example, we can measure the spacing of forest trees, irrespective of their species.

STATISTICAL TREATMENT OF MEASUREMENTS OF SPACING

The site which each individual organism occupies in its habitat covers a certain amount of space. When any individual is taken as a point of origin for measuring spacing, the number of possible sites for other individuals of the same species increases as the square of the distance from the point of origin. In treating statistically the measurements of spacing between individuals, consequently, the square-root transformation of the measurements will be appropriate. Means, variances, standard deviations, standard errors, and other similar statistics, therefore, may be calculated from the square roots of the measurements of the spacing between individuals taken according to the method described in the previous section.

The variability of the measurements of spacing may be measured by variance, standard deviation, or coefficient of variation in the usual fashion. When, however, the frequency curve of the measurements of spacing is skewed, as is true for many natural populations, then the variance and the statistics calculated from it may not give a fully reliable measure of variability.

RELATION OF TYPE OF DISTRIBUTION TO SPACING BETWEEN INDIVIDUALS

The distances that separate the individuals within any population are affected by their type of distribution. When the individuals are evenly distributed the measurements of the distances between them will have little if any variability. Should the individuals be irregularly distributed over the habitat the measurements of their spacing may be highly variable.

Uniform Distribution

Let us first consider a population in which the individuals are equally spaced over a plane. For such a distribution the maximum population density per unit of area will be obtained when the individuals are distributed in a triangular pattern (Fig. 1). In such a distribution any given individual is equally distant from the 6 nearest adjacent individuals (Cottam and Curtis, 1949). If one selects any particular individual as a point of origin and measures the distance to the nearest adjacent individual in each of the 6 surrounding sextants, 6 identical measurements will be obtained.

The reason for measuring to the nearest individual in each sextant surrounding the point of origin will now be evident. By so doing one obtains a variance of zero under conditions of even spacing between individuals. Any departure from uniform distribution will be indicated, therefore, by the variance. A tendency toward even spacing, moreover, will produce a frequency curve of the square roots of the measurements of spacing which will be skewed to the right. The g_1 statistic of such a curve will have a negative value.

An approach toward uniform spacing is likely to occur in any population where there is severe competition between the individuals for sunlight, moisture, or some other essential factor which is present in limited supply. Animals that maintain territories, for example, tend to be distributed more evenly than random.

As an illustration of spacing that tends to be more regular than random, Figure 3 shows the frequency polygon for the square roots of the measurements of the spacing of forest trees within a certain grove. The trees considered in these measurements are only those which are of sufficient height to have become part of the forest canopy. Forest trees are in strong competition for sunlight and consequently they tend to be spaced at more regular intervals than random. In accordance with this expectation we find the frequency polygon of the measurements of the spacing of these trees to be skewed to the right. The amount of the skewness, as measured by g_1, is -0.27, which has a t value slightly below the 5 per cent level of significance (Table I). The g_2 measure of kurtosis is

TABLE I

Square Roots of Measurements (by Sextants) of Spacing Between Individual Plants of Certain Species Growing on the Edwin S. George Reserve, Livingston County, Michigan; also of Dots Distributed at Random Over a Plane Surface

		Square Roots of Measurements of Spacing					
Plant	Number of Measurements	Mean $\sqrt{cm}$	Standard Deviation	g_1	t_1	g_2	t_2
Hieracium ...	294	8.09 ± .20	3.52	.96	6.75	....	....
Lespedeza ...	274	12.63 ± .48	7.90	2.25	15.30	....	....
Liatris	430	17.26 ± .51	10.73	1.14	9.74	....	....
Solidago	251	17.96 ± .50	7.87	.84	5.46	....	....
Forest trees .	300	21.39 ± .28	4.79	-.27	-1.92	-.04	-.14
Solidago → Liatris ...	246	28.70 ± .70	10.90	.02	.14	-.59	-1.90
Liatris → Solidago...	248	27.30 ± .59	9.29	.06	.39	-.49	-1.59
Random dots .	294	$\sqrt{unit}$ 2.22 ± .04	.64	.11	.77	-.50	-1.76

-0.04, which is insignificant. The forest measured was young, however, and was composed mostly of second-growth oaks and hickories. A more mature forest might be expected to be still more regularly distributed and to have a still greater negative value of g_1.

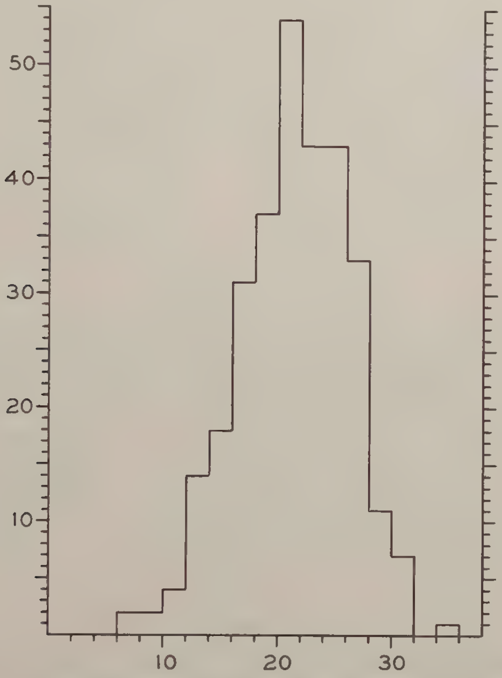


FIG. 3. Frequency polygon for the square roots of the measurements by sextants between those forest trees which extend into the forest crown in an oak-hickory grove on the Edwin S. George Reserve, Livingston County, Michigan.

Random Distribution

In order to measure the spacing in a population of individuals distributed at random over a plane surface a population of dots was placed on a sheet of cross-section paper. Each vertical and horizontal line on the paper was numbered and the positions of 500 dots were located by drawing from a table of random numbers. Fifty of these randomly distributed dots were drawn at random as points of origin for the measurements of spacing. From these points of origin, the distance to the nearest other dot in each surrounding sextant was measured, in accordance with the method previously described (Fig. 4). The frequency polygon for the square roots of these measurements is presented in Figure 5.

Owing to the method of placing the dots on the sheet of cross-section paper, no dots were closer together than 1.0 unit, and consequently the frequency curve of the square roots of the measurements of the spacing between dots is truncated at its lower end. Aside from this

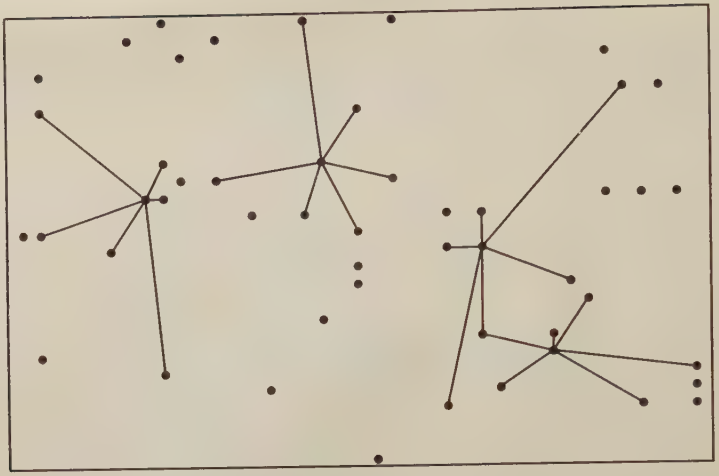


FIG. 4. Part of a sheet on which dots have been placed at random. It illustrates the method of taking measurements to the nearest dots in the sextants surrounding each of 4 dots taken at random as points of origin.

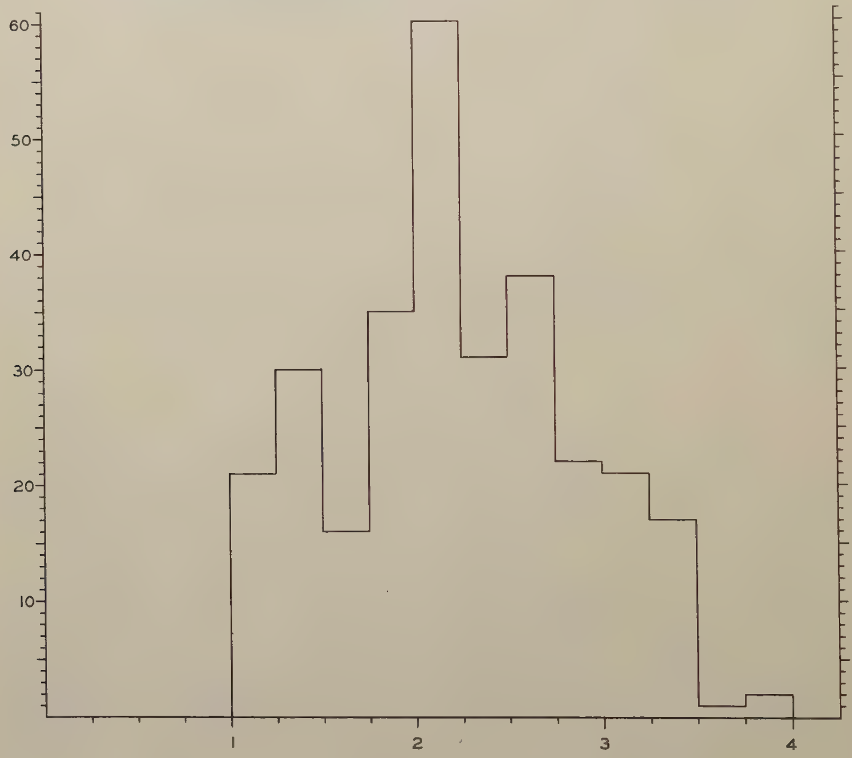


FIG. 5. Frequency polygon of square roots of spacing by sextants between 500 dots distributed at random over a sheet of cross-section paper, 100 x 100 units in area. Fifty dots were taken at random as points of origin for the measurements, which were by sextants. Incomplete and duplicate measurements not included.

discrepancy, the frequency polygon seems not to depart seriously from a normal curve. There is a negligible amount of skewness, as shown by a g_1 of 0.11. The small amount of kurtosis ($g_2 = -0.50$, $t_2 = -1.76$) is probably caused by the truncation of the lower end of the frequency curve. George W. Thomson has kindly recalculated these measures of the spacing of random dots on the assumption that they constitute a truncated sample from a randomly distributed population, using the method of Cohen (1950), and finds excellent agreement with expectation for a normal curve. It may be concluded, therefore, that the frequencies of the square roots of the distances between individuals of a randomly distributed population, when measured by the method described above, approach a normal curve.

Clumped Distribution

The individuals of many natural populations are distributed in more or less compact aggregations. Such aggregations may be produced by a tendency of the individuals to remain near their site of origin, by social attraction between the individuals, by the accumulation of the individuals in particularly favorable local situations, or perhaps by other causes. The aggregations composed of the individuals of certain species may be tightly clumped, leaving extensive unoccupied spaces between the aggregations. On the contrary, the aggregations of other species may be very loose, so that the distribution departs only slightly from random.

When any considerable tendency toward clumping is present in a population distributed over a plane surface, the frequency curve of the square roots of the measurements of spacing between the individuals, taken according to the method here proposed, will be skewed toward the left. This is illustrated in Figures 6 to 9, which are based on measurements of the spacing of the individuals of 4 species of plants.

The significance of the skewness of a frequency curve can be evaluated from g_1, which is calculated from the third moments of the deviations from the mean. From Table I it will be seen that Lespedeza has the highest g_1 value (2.25), Liatris (1.14) is next, then Hieracium (0.96), while Solidago (0.84) has the lowest g_1 value of the 4 plant species whose distributional patterns are here compared. The departure of each of these species of plants from a random distribution, as measured by t, is highly significant. All of these plants are noticeably clumped in nature. Solidago is less strongly clumped than Liatris and Lespedeza is more strongly clumped than either of these 2 species (Thomson, 1952). For these 3 species, therefore, the magnitudes of the g_1 values of their measurements of spacing fall in the same order as their degree of clumping. I have no estimate of the degree of clumping in the field of Hieracium, as compared to that of the other 3 species of plants. I conclude that the g_1 statistic is useful for measuring the significance of the departure of any distribution from randomness and that it may also give a rough measure of the strength of clumping.

Any attempt to specify the type of distribution of an irregularly spaced population by a single statistic, however, seems likely to be futile. The spacing of individuals in a population exhibits many diverse types of irregularities. The spacing of the individuals within each aggregation may be uniform, random, or irregular. The density of the aggregations may vary from compact to loose. The boundaries of the several aggregations may vary from sharp to indistinct. The aggregations themselves also may be distributed evenly, at random, or very irregularly. Furthermore, there may be various degrees of secondary or even tertiary clumping within the major aggregations. Measures of skewness and of kurtosis will often assist in the analysis of distribution, but such statistics cannot be expected to give a complete description of the organization of a complex population.

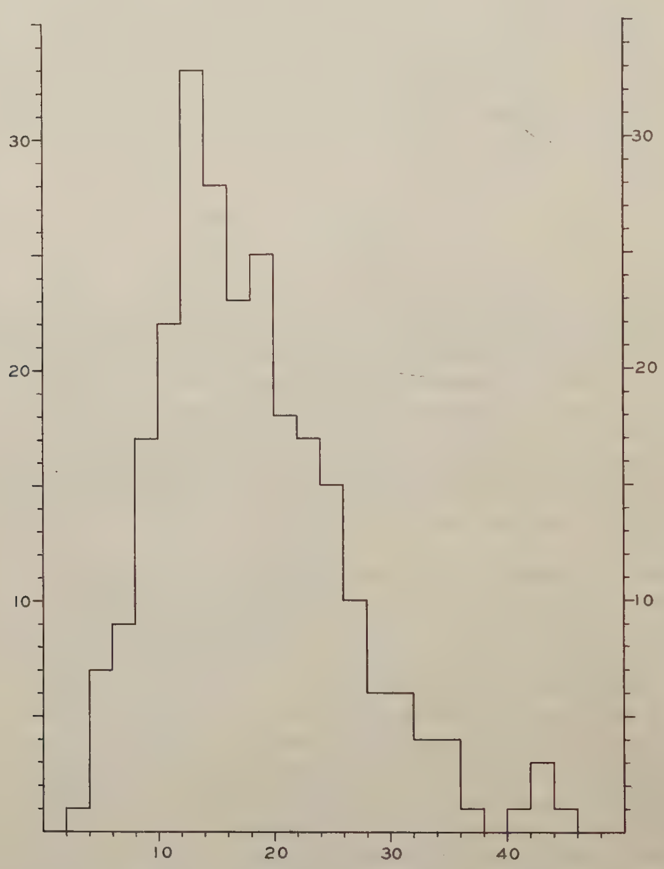


FIG. 6. Frequency polygon for the square roots of the spacing between individuals of Solidago rigida on a grassy area on the Edwin S. George Reserve, Livingston County, Michigan, as plotted by Cain and Evans (1952). Measurements taken by sextants. Incomplete and duplicate measurements omitted.

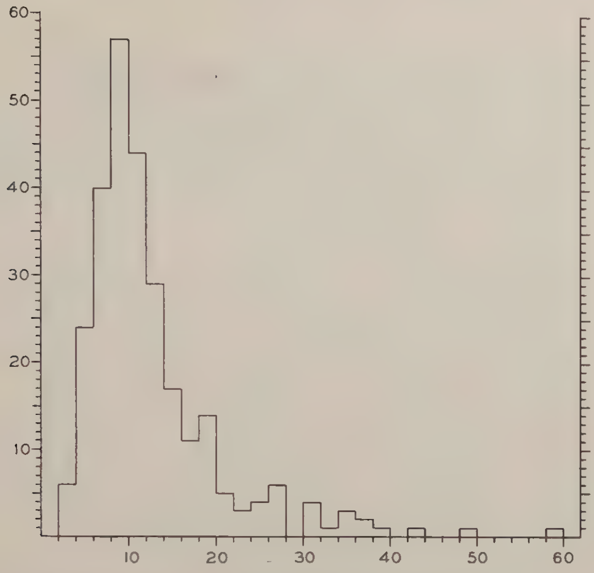


FIG. 7. Frequency polygon for the square roots of the spacing between individuals of Lespedeza capitata on a grassy area on the Edwin S. George Reserve, Livingston County, Michigan, as plotted by Cain and Evans (1952). Measurements taken by sextants. Incomplete and duplicate measurements omitted.

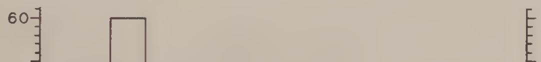


FIG. 8. Frequency polygon for the square roots of the spacing between individuals of Liatris aspera on a grassy area on the Edwin S. George Reserve, Livingston County, Michigan, as plotted by Cain and Evans (1952). Measurements taken by sextants. Incomplete and duplicate measurements omitted.

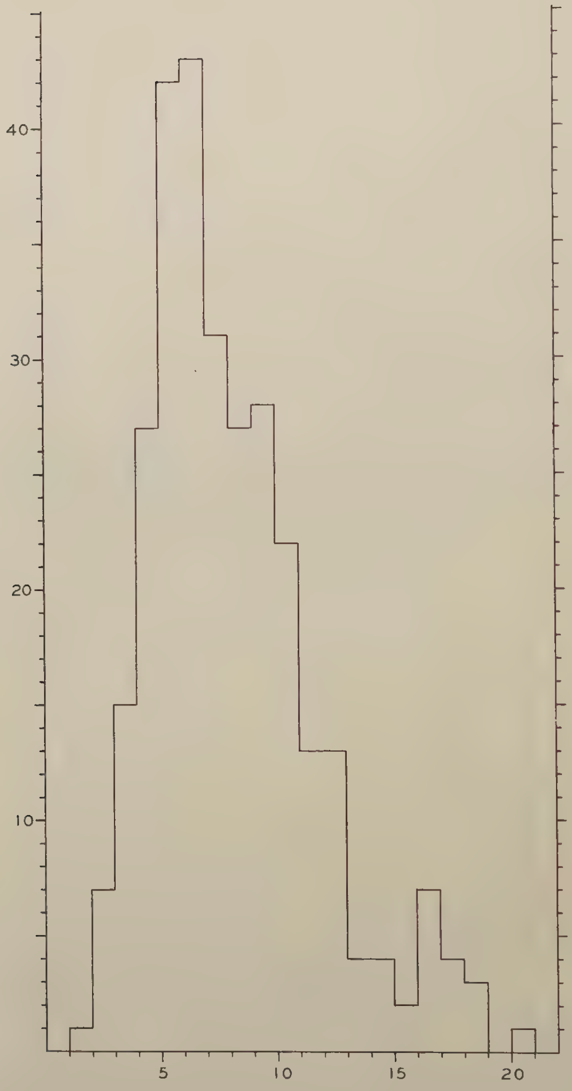


FIG. 9. Frequency polygon for the square roots of the spacing between individuals of Hieracium longipilum on a grassy plot on the Edwin S. George Reserve, Livingston County, Michigan. Measurements taken by sextants. Incomplete and duplicate measurements omitted.

When the individuals of a population occur in compact clumps with completely unoccupied spaces separating the clumps, then the measurements of spacing between the individuals will form a bimodal curve. That this must be so is demonstrated in Figure 10, in which a hypothetical population of dots is distributed in clumps of 7, the individual dots within the clumps and the clumps themselves being evenly spaced apart. If the middle individual in any clump is taken as a point of origin, all the measurements of spacing, taken by sextants according to the method here proposed, will be equal. On the other hand, if an individual at the edge of a clump is taken as the point of origin, the measurements of spacing will be of 2 types, those to other individuals within the same clump, and those to the nearest individuals in adjacent clumps. The square roots of such measurements will form a bimodal curve, one mode representing the square roots of the spacing of the individuals within the clumps, the other mode representing the square roots of the spacing between the outside individuals of adjacent clumps.

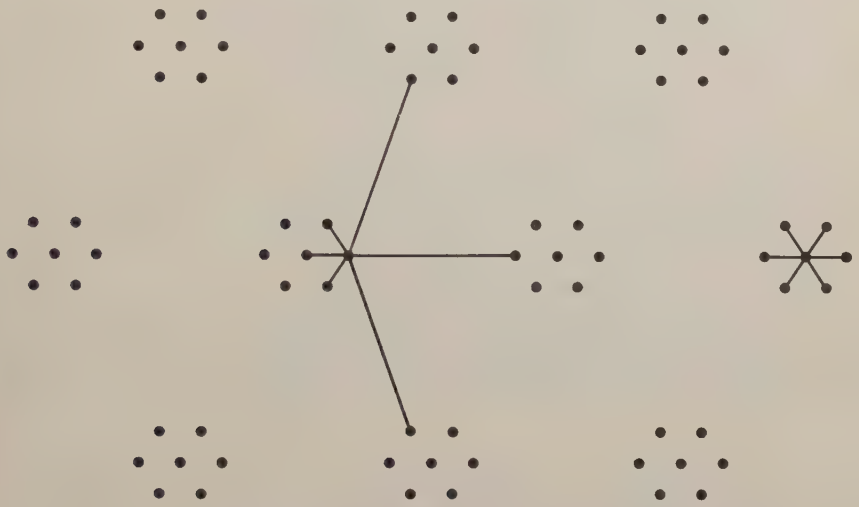


FIG. 10. Measurements of spacing by sextants from individuals in a population of dots, which are distributed uniformly in clumps of 7, with the clumps evenly spaced apart.

In nature such a simple type of clumped distribution will never be encountered. The distances between clumps is certain to be variable, as well as the spacing of the individuals within the clumps. It will usually be more practical in the field to measure directly the spacing between clumps, rather than to estimate such spacing from measurements between individuals. Nevertheless, whenever a bimodal curve of the spacing within a population is encountered, it will indicate a tendency of the individuals to occur in compact and discrete clumps.

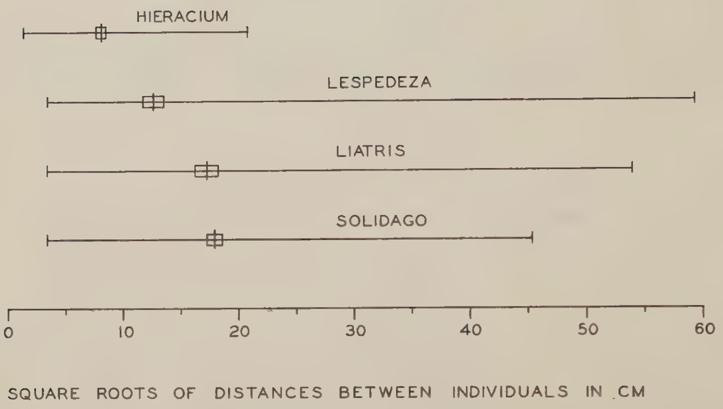


FIG. 11. Comparison between the spacing of 4 species of herbs on the Edwin S. George Reserve, Livingston County, Michigan, according to the method of Dice and Leraas (1936). For each species the length of the line gives the extremes of the square roots of the measurements, the heavy cross bar indicates the mean, the rectangle extends twice the standard error on each side of the mean.

Distribution in Three-dimensional Space

The spacing between individuals distributed in 3-dimensional space could be measured in somewhat the same manner as between individuals all of which lie on a single plane. It should thus be possible to measure the spacing between individual plants or animals that occupy different strata in a community. The making of measurements in 3-dimensional space, however, and the statistical treatment of such measurements would require special procedures which will not be considered in this paper.

COMPARISON OF SPACING IN DIFFERENT POPULATIONS

The means of the square roots of the spacing between the individuals in any 2 populations may be compared by the usual statistical method, which employs the standard error of the mean and its t value. Even though the 2 frequency curves may be skewed, their standard errors nevertheless are usually reliable as a basis for testing significance. In Figure 11 is presented a graphic comparison of the mean spacing of the 4 species of plants measured on the George Reserve. It is evident from this figure that Hieracium has a significantly lesser mean distance between individuals than any of the other species. The spacing of Liatris does not differ significantly from that of Solidago, but the average spacing between the individuals of both these species is significantly greater than that between the individuals of Lespedeza.

RELATIONSHIP BETWEEN SPACING AND POPULATION DENSITY

The density of a population in which the individuals are uniformly spaced and as densely packed as possible (Fig. 3) is inversely related to the square of the distance between individuals. In such a triangular distribution each individual occupies 0.866 of a square unit of the distance between individuals. Expressed in another way, there are 1.155 individuals per square unit. If we let S be the average distance in any standard units between the adjacent individuals of such a population and let P be the average population density per square unit of measurement, then:

$$P = 1.155/S^2, \text{ and } S = \sqrt{1.155/P} .$$

These formulas seem also to be applicable to populations which are distributed at random. For example, on the sheet of cross-section paper 100 x 100 units square, on which 500 dots were placed at random, as described above, the density of the dots was 0.05 per square unit. The mean spacing between dots should, therefore, be:

$$S = \sqrt{1.155/0.55} = \sqrt{23.100} = 4.806 .$$

The square root of the expected mean spacing between dots is 2.19. The actual mean of the square roots of the measurements of spacing between dots, taken by sextants, is 2.22 ± .04 (Table II), which does not differ

TABLE II

Comparison Between Calculated and Measured Spacing (by Sextants) in Populations Having Various Types of Distribution and with Dots Distributed at Random.

Plant	Mean Density Per m²	Square Roots of Mean Spacing				Calculated Minus Measured $\sqrt{\text{cm}}$
		Calculated from Density $\sqrt{\text{cm}}$	Actual Measurements $\sqrt{\text{cm}}$	g_1	g_2	
Hieracium	1.765	8.99	8.09 ± .20	.96	...	.90
Lespedeza	.108	18.10	12.63 ± .48	2.25	...	5.47
Liatris	.041	22.98	17.26 ± .51	1.14	...	5.72
Solidago	.064	20.61	17.96 ± .50	.84	...	2.65
Forest trees ..	.064	20.59	21.39 ± .28	-.27	-.04	-.80
Solidago → Liatris	.042	22.96	28.70 ± .70	.02	-.59	-5.74
Liatris → Solidago	.064	20.60	27.30 ± .59	.06	-.49	-6.70
	Per unit²	$\sqrt{\text{units}}$	$\sqrt{\text{units}}$			$\sqrt{\text{units}}$
Random dots ..	.050	2.19	2.22 ± .04	.11	-.50	-.03

significantly from the spacing calculated from the density according to the above formula. The measured spacing of forest trees (Table II), also agrees closely with the spacing calculated from the density according to the formula.

In populations in which frequency curves of the square roots of the measurements of spacing are strongly skewed either to the right or to the left, however, these formulas give answers which disagree considerably with the actual measurements of spacing. The expected mean spacing, calculated from their densities, for all kinds of plants listed in Table II depart considerably from the actual measurements of spacing taken by sextants. For those species whose individuals tend to be clumped in distribution, as shown by positive g_1 values, the measured spacings are less than the calculated ones. For the forest trees, however, which are somewhat more evenly distributed than random, as shown by a negative g_1 value, the spacing calculated from the density is less than the measured spacing. There is moreover, no close correlation between the g_1 value and the degree of difference between the expected spacing calculated from the density, and the actual measurements of spacing. Inasmuch as a large number of organisms in nature have nonrandom distributions, any general attempt to estimate spacing from population density, or the reverse, will evidently be impractical.

SPACING AS A MEASURE OF ASSOCIATION BETWEEN SPECIES

Several quantitative methods have been developed to measure the amount of association between 2 species (Forbes, 1907; Dice, 1945; Cole, 1949). These methods have been based on counts of the frequency of occurrence of the species being compared on sample plots or in samples of other kinds. The measures of association which are thus obtained have the disadvantage that they are gravely affected by the sizes of the samples (Nash, 1950). This difficulty could be in part avoided if we could base our comparisons on measurements of the spacing between the individuals of those pairs of species whose association is in question.

In order to develop such a method, let us assume that the members of a given species, alpha, are distributed over an area at random. Then, as pointed out above, the square roots of the distances between the individuals of this species, measured by sextants, will approach a normal curve. If now we add, also at random, an individual of another species, beta, and from this individual as a point of origin measure the distance to the nearest alpha individual in each surrounding sextant, then the square roots of these measurements will also form a normal curve. This will be true because the addition of another individual at random to the population will not change the random nature of the distribution. The only effect of adding the one individual of beta is to increase the previous population by one individual. Such an addition will decrease by a correspondingly slight amount the mean spacing between the individuals of the combined population. The square roots of the measurements, taken by sextants, of the spacing from any number of randomly distributed individuals of species beta, taken one at a time as points of origin, to the nearest individuals of a randomly distributed species alpha, will consequently approach a normal curve.

Should one of the species of a pair whose association is being measured be considerably more abundant than the other species, then the measurements should always be made from the individuals of the rarer species. Should the individuals of the more abundant species be taken as points of origin for the measurements of spacing, no individual of the rarer species might happen to occur nearby. Under these conditions the frequencies of the square roots of the measurements might approach a normal curve, even though the rare species may actually be closely associated with the more abundant one.

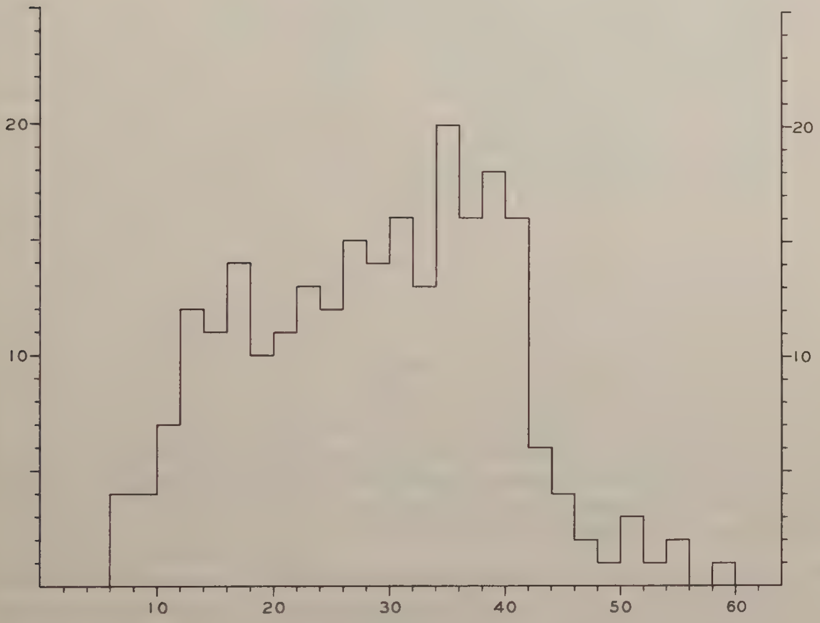


FIG. 12. Frequency polygon of square roots of distances from 50 individuals of Solidago rigida, taken as points of origin, to the nearest individual of Liatris aspera in each surrounding sextant. Measurements taken on chart constructed by Cain and Evans (1952) of the distribution of these plants over a grassy area on the Edwin S. George Reserve, Livingston County, Michigan.

As an application of the proposed method, I have measured the spacing between Solidago and Liatris on the plot on the George Reserve previously described. From the population of Solidago certain individuals were taken at random as points of origin for the first set of measurements. From each such point of origin, the distance in each surrounding sextant to the nearest individual of Liatris was measured. The square roots of these measurements form a nearly symmetrical frequency curve (Fig. 12) whose g_1 value is only an insignificant 0.02.

The curve, however, exhibits a moderate amount of negative kurtosis, the g_2 value being -0.59, which is just below the 5 per cent level of significance (Table I). The top of the curve is noticeably plateau-like.

A similar result is obtained when we use individual plants of Liatris as the points of origin and measure to the nearest plants of Solidago in each surrounding sextant (Fig. 13). Again the g_1 statistic of the square roots of the measurements has only an insignificant value, indicating absence of skewness, but g_2 has again a negative value, this time, however, well below the 5 per cent level of significance (Table I).

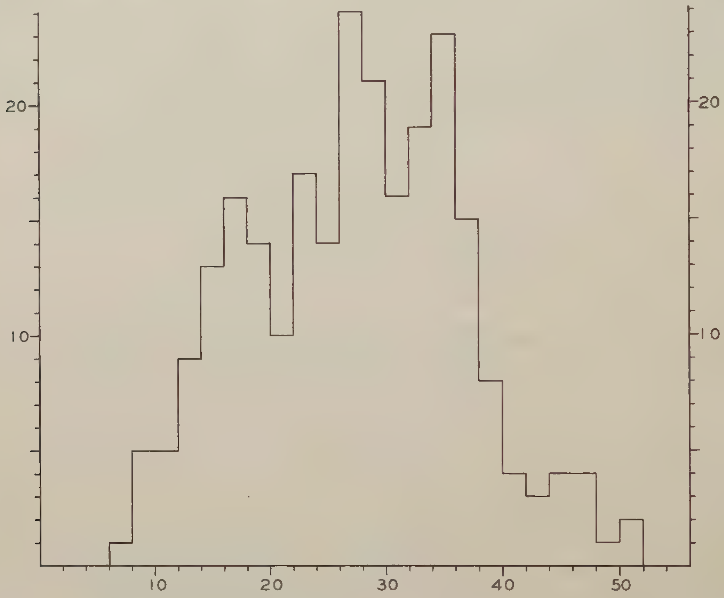


FIG. 13. Frequency polygon of square roots of distances from 50 individuals of Liatris aspera, taken as points of origin, to the nearest individual of Solidago rigida in each surrounding sextant. Measurements taken on a chart constructed by Cain and Evans (1952) of the distribution of these plants over a grassy area on the Edwin S. George Reserve, Livingston County, Michigan.

I interpret the absence of skewness in the square roots of the measurements of the spacing between Liatris and Solidago to indicate the absence of any tendency toward either association or repulsion between the individuals of these 2 species. It will readily be agreed, however, that the association between a sufficient number of pairs of species has not as yet been measured by this method to be certain that absence of skewness will always indicate lack of association.

The significance of the departure from normality of the frequency curve of the square roots of the measurements by sextants of spacing between the individuals of 2 species can be tested by the g_1 statistic. Skewness to the left (g_1 positive) should indicate a tendency toward association between the 2 species, while skewness to the right (g_1 negative) should indicate repulsion. Unfortunately, I have at hand no example either of positive or negative skewness of the frequency curves of such interspecies measurements of spacing.

The presence of negative kurtosis in the frequency curves of the square roots of the distances from Solidago to Liatris and also from Liatris to Solidago is perhaps related to the fact that both these species are clumped in distribution. The points of origin for the measurements of spacing are consequently not taken completely at random, but also are clumped. In order to be sure whether this is a true explanation of the negative kurtosis in these frequency curves further studies will be needed. For the present I am assuming that this negative kurtosis does not indicate any tendency toward association or repulsion between the individuals of the 2 species

Another possible measure of association between 2 species might be presumed to be given by the expected spacing between them calculated from the density, compared with the actual measured spacing between the individuals. The measured mean spacing, however, both of Solidago to Liatris and of Liatris to Solidago departs seriously from the mean spacing calculated from the densities of these plants (Table II.) Perhaps this discrepancy is due to the negative kurtosis exhibited by the frequency curves of the interspecies measurements of spacing. Whatever the cause of the discrepancy, when one or both members of a pair of species are nonrandom in distribution, the expected mean spacing between them calculated from their density compared with the mean spacing obtained from actual measurements does not give a reliable measure of association.

Much more study will be needed to test the value of measures of interspecies spacing as an indicator of association or repulsion between the members of a pair of species. The scanty evidence at hand indicates that the g_1 statistic of measurements of interspecies spacing taken by sextants can be used as a test of the reliability of any tendency toward association or repulsion between the individuals. It is not anticipated, however, that g_1 or any other simple statistic can measure the strength of association between 2 given species. The individuals of 2 associated species may be related to one another in so many possible ways that no simple measure is likely to be adequate to describe every possible combination.

SUMMARY

For measuring the spacing between the individuals in any given population which is distributed over a single plane the following method is proposed: (1) A certain number of individuals in the population are taken at random as points of origin for the measurements. (2) From each such point of origin the distance is measured in each surrounding sextant to the nearest other individual in the same population. (3) The square roots of these measurements of spacing are treated statistically to derive means, variances, and other statistics.

The frequency curve of the square roots of the measurements of the spacing between individuals, taken according to the above described method, approaches normality when the distribution of the population is random. When the individuals are clumped, the curve is skewed toward the left. When the distribution is more even than random, the curve is skewed toward the right. The significance of any irregularity of distribution may be evaluated by the g_1 and g_2 statistics. These statistics, moreover, give a measure of the degree of departure of any distribution from randomness.

The relations between mean population density per unit area (P) and the mean spacing between the individuals (S) measured by sextants should be given by the formulas: (1) $P = 1.155/S^2$ and (2) $S = \sqrt{1.155/P}$. These formulas seem to apply with fair precision when the distribution of the individuals in a population is approximately random or is more even than random, but they give erroneous values when the individuals occur in aggregations.

The square roots of the measurements of spacing between the individuals of one species, taken at random as points of origin, to the nearest individuals of another species in each surrounding sextant should approach a normal frequency curve when there is no association between the 2 species. The curve is expected to be skewed to the left when there is association between the members of the 2 species, or to the right when there is repulsion between them. The significance of any tendency toward association or repulsion can then be measured by the g_1 statistic. The frequency curves of the square roots of the measurements of the spacing between 2 species, each of which is clumped in distribution, however, exhibit negative kurtosis.

The measurement of spacing between individuals should be of general usefulness for describing the structure of populations and communities in quantitative terms. Its particular merit is that the measurements obtained are not affected by sample size.

LITERATURE CITED

BEALL, GEOFFREY

1935 Study of arthropod populations by the method of sweeping. Ecology, 16:216-25.

CAIN, STANLEY C., and FRANCIS C. EVANS

1952 Distribution of three plant species in an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 52.

CLAPHAM, A. R.

1936 Over-dispersion in grassland communities and the use of statistical methods in ecology. Journ. Ecol., 24: 232-51.

COHEN, A. C., Jr.

1950 Estimating parameters of Pearson Type III populations from truncated samples. Journ. Amer. Statis. Assn., 45: 411-23.

COLE, LAMONT C.

1946 A study of the cryptozoa of an Illinois woodland. Ecol. Monog., 16: 49-86.

1949 The measurement of interspecific association. Ecology, 30: 411-29.

COTTAM, GRANT, and J. T. CURTIS

1949 A method for making rapid surveys of woodlands by means of pairs of randomly selected trees. Ecology, 30: 101-104.

DICE, LEE R.

1945 Measures of the amount of ecologic association between species. Ecology, 26: 297-302.

DICE, LEE R., and HAROLD J. LERAAS

1936 A graphic method for comparing several sets of measurements. Contrib. Lab. Vert. Gen. Univ. Mich., 3: 1-3.

EVANS, FRANCIS C.

1952 Influence of size of quadrat on the distributional patterns of plant populations. Contrib. Lab. Vert. Biol. Univ. Mich., 54:

EVANS, FRANCIS C., and STANLEY A. CAIN

1952 Preliminary studies on the vegetation of an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 51:

FISHER, ARNE

1915 The mathematical theory of probabilities and its application to frequency curves and statistical methods. New York: Macmillan Co.

FORBES, S. A.

1907 On the local distribution of certain Illinois fishes: an essay in statistical ecology. Bull. Illinois State Lab. Nat. Hist., 7: 273-303.

NASH, CARROLL BLUE

1950 Associations between fish species in tributaries and shore waters of western Lake Erie. Ecology, 31: 561-66.

RAUNKIAER, C.

1934 The area of dominance, species density, and formation dominants. In: The life forms of plants and statistical plant geography. Oxford: Clarendon Press, pp. 517-46.

THOMSON, GEORGE W.

1952 Measures of plant aggregation based on contagious distributions. Contrib. Lab. Vert. Biol. Univ. Mich. 53.

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price $0.35.

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

University of Michigan, Ann Arbor, Michigan

Number 56 May, 1952

AN EXPERIMENTAL STUDY OF HABITAT SELECTION BY PRAIRIE AND FOREST RACES OF THE DEERMOUSE, PEROMYSCUS MANICULATUS

By VAN T. HARRIS

Accepted for publication June 15, 1951

CONTENTS

Introduction 1
Methods and Materials 2
Statistical Analysis 10
Descriptions and Results of the Experiments 14
Factors Which May Have Influenced Results of the Experiments 34
Reliability and Variability in Selection of Artificial Habitats 38
Factors Selected in the Habitat 42
Heredity of Habitat Selection 47
Summary 49
Literature Cited 50

INTRODUCTION

ANIMALS are not distributed at random over the surface of the earth. Each species is restricted in the extent of its distribution by the limits of its physiological tolerances to the physical and biological factors of its environment. A species, however, rarely occurs everywhere within the geographical area fixed by these tolerances. Every species is more or less restricted to certain habitats within its geographical range, though it may not live in all those habitats that appear to be similar. Each kind of animal evidently prefers a certain type of habitat to other types and consequently must have some means of selecting the one preferred.

The purpose of the investigation herein reported was to study and to measure some of the factors governing the selection of habitats by small mammals. The experimental animals, Peromyscus maniculatus gracilis, the forest deermouse, and P. m. bairdi, the prairie deermouse, were chosen for study because of their rather definite habitat restrictions in nature and because of their availability in the laboratory. The investigation was carried out under laboratory conditions in order to control more precisely the many factors in the animals' environments. The approach was psychological in that 2 different habitats were presented to the mice for selection in each experiment.

Acknowledgments

This study was carried out under the direction of Professor Lee R. Dice to whom I wish to express my appreciation. Dr. C. C. Craig and other members of the Statistical Research Laboratory, University of Michigan, guided me in the statistical analysis of the data, and Dr. Craig adapted the theory of estimation of missing values to the particular analysis presented herein. Advice and suggestions in statistical matters were also given by Dr. C. W. Cotterman. Philip J. Clark made tests on mice during my absence. The Laboratory of Vertebrate Biology, University of Michigan, provided the reaction room and supported the study with materials, equipment, and experimental animals.

METHODS AND MATERIALS

Description of the Reaction Room

The experiments were conducted in the reaction room of the Laboratory of Vertebrate Biology. A sheet-metal partition 24 inches high divided this room into 2 compartments, each 9 by 10 1/2 feet. The room was nearly light tight and was painted a flat black on the inside. Air ducts leading into the room were equipped with light traps. Ventilation was provided by a fan which blew air into one end of the room through a duct near the ceiling. The air passed out through a similar duct at the other end of the room. The door was near one end of the room.

The lights were connected with a control panel which was outside the room. An electric light socket on the ceiling over the middle of each compartment was equipped to provide various low intensities of light by use of paper disks fastened below the bulb (Dice, 1945:386). Each central fixture in the 2 compartments was surrounded by a cluster of 3 light sockets. These 6 lights were wired through a time clock on the control panel. With this equipment alternating periods of bright light and of dim light or darkness could be produced in the room.

Artificial Habitats

In order to place the study of habitat selection on an experimental basis, standardized and to some extent simplified objects were provided to simulate the vegetational forms present in natural habitats.

The principal features of the artificial forest or tree-trunk habitat (Pl. I, Fig. 1) comprised 9 sections of tree trunks with bark adhering. These trunks varied in height from 20 to 48 inches and in diameter from 2 to 10 inches.

Artificial grass was made from stiff Manila folders. Each half of a folder (9 by 12 inches) was cut into strips about 3/8 inch wide for almost its whole length. The uncut part of each half folder, with the cut strips attached, was then rolled and fastened with Scotch tape, so that its base formed a short cylinder. The pointed end of a nail, driven completely through a lath, formed a support for the cylinder which was inserted over the nail. When the cylinder was placed in an upright position on the lath, the free ends of the cut strips drooped over to resemble a tuft of grass. These tufts of artificial grass were placed at intervals along the lath, and the laths were placed in the compartment about 1 foot apart in parallel formation. One open spot of a few square feet was left near the center of the compartment, as well as a path along 1 side. Otherwise, the tufts of artificial grass covered the floor of a compartment to provide the artificial-grass habitat (Pl. I, Fig. 2).

An intermediate type of habitat resembling a stylized form of shrubbery was provided by the "jungles" developed and described by Dice (1947:8). These were made of strips of wood, as shown in Plate II, Figure 1. The jungles were spaced to cover most of the floor of a compartment, leaving aisles by which the compartment could be entered.

White silica sand covered the floors of the compartments in all the experiments. Besides providing for the mice a more natural floor than the cement, it recorded their tracks and thus gave information about their activity.

Methods of Measuring Habitat Selection

Habitat selection by the mice of the 2 subspecies of Peromyscus tested in the experiments was measured by (1) the amount of food eaten, (2) the amount of water consumed, (3) the number of revolutions made in the activity wheel, and (4) the total time spent in each of the 2 artificial habitats. A food dish, a water tube, a nest box, and an activity wheel were placed in corresponding positions in each compartment.

A definite number of sunflower seeds was counted every day into each food dish. The mice sometimes removed many of these seeds and stored them under the sand. The number of seeds eaten was ascertained by counting the number of whole seeds in the dish, adding the number eaten as estimated from the empty shells, and then, if the original number was not accounted for, searching for those that were stored. Looking for the stored seeds was not entirely a random process since many mice preferred certain spots for storing, and buried seeds could often be detected by the disturbed and heaped-up sand. The error of this estimation for seeds eaten seldom exceeded 2 or 3 per cent. If, according to this estimate, too many seeds seemed to be missing, the data were discarded. By this method one could also ascertain if seeds were carried from one compartment to the other. Actual evidence for this was rarely obtained.

Water tubes were made by sealing the open ends of ordinary culture tubes to openings of about 3 mm. in diameter. Each tube was held by a wire clamp and was hung on a rack with the open end down (Pl. II, Fig. 2). The amount of water consumed by each mouse each day could be determined by refilling the tube from a burette graduated to 0.2 ml. As thus measured, the amount of water consumed included evaporation from the tubes, which averaged about 0.2 ml. per day.

The activity wheels (Pl. I, Fig. 2) were adapted by Sumner (1932:91) from a design by Richter and Wang (1926). Each was constructed of a plywood disk about 9 inches in diameter around which was fastened a piece of hardware cloth 4 3/4 inches wide. The wheel, which weighed approximately 350 gm., was mounted on a ball-bearing axle fastened to a standard and was equipped with a counter that recorded the number of revolutions. An opening through the standard led to the inside of the wheel. The number of revolutions made by the mouse was recorded each day, and the counter was then reset at zero.

Nest boxes were made from aluminum saucepans 6 inches in diameter and 2 1/2 inches deep (Dice, 1929:119). An entrance was cut from the side of a saucepan which was inverted over a piece of masonite. The box was then provided with a small amount of cotton for nesting material.

Apparatus for Recording Time Spent in Each Compartment

To allow the mice access to both compartments, a runway was built over the partition which divided the room. The base of the middle section of the runway consisted of a board that rested horizontally across the partition. At each end it was connected with the floor by a sloping board about 33 inches long. The sloping boards were covered with fine wire screen to make climbing easier for the mice.

The horizontal part of the runway was enclosed by sheet-metal sides and a transparent celluloid top (Pl. I, Fig. 1). The latter was intended to prevent the runway from becoming a darkened retreat attractive to the mice. Each end of the enclosed part was surrounded by shields placed perpendicular to the entrance to prevent the mice from jumping to the partition of the room from the sloping part of the runway.

The enclosed middle section of the runway contained the electrical contact mechanism (Fig. 1) which reported the movements of the mice in the runway to the recording apparatus outside the room.

To travel from one compartment to the other a mouse was required to pass through 2 swinging screen doors which hung down into the passageway. When a door was pushed open, the arm of the door made a contact with a pliant brass strip and closed an electrical circuit to the recording apparatus. This circuit energized an electromagnet which attracted 1 end of the horizontal arm of the recording apparatus built on the plan of a kymograph penholder. The contact made by the doors may have been momentary, and the attracting force of the electromagnet may thus have been of short duration, but a locking device prevented the arm of the recording apparatus from bouncing.

When the mouse again passed through the runway apparatus on its way to the other compartment, the door which last made contact was pushed open toward the center of the enclosed runway, and the electric circuit was not closed except perhaps momentarily as the door swung back into place. No change in record occurred, however, because the horizontal arm of the recording apparatus was already against the electromagnet controlled by this door. As the mouse proceeded on its way, it pushed open the door leading to the other compartment, thus closing the circuit to the corresponding

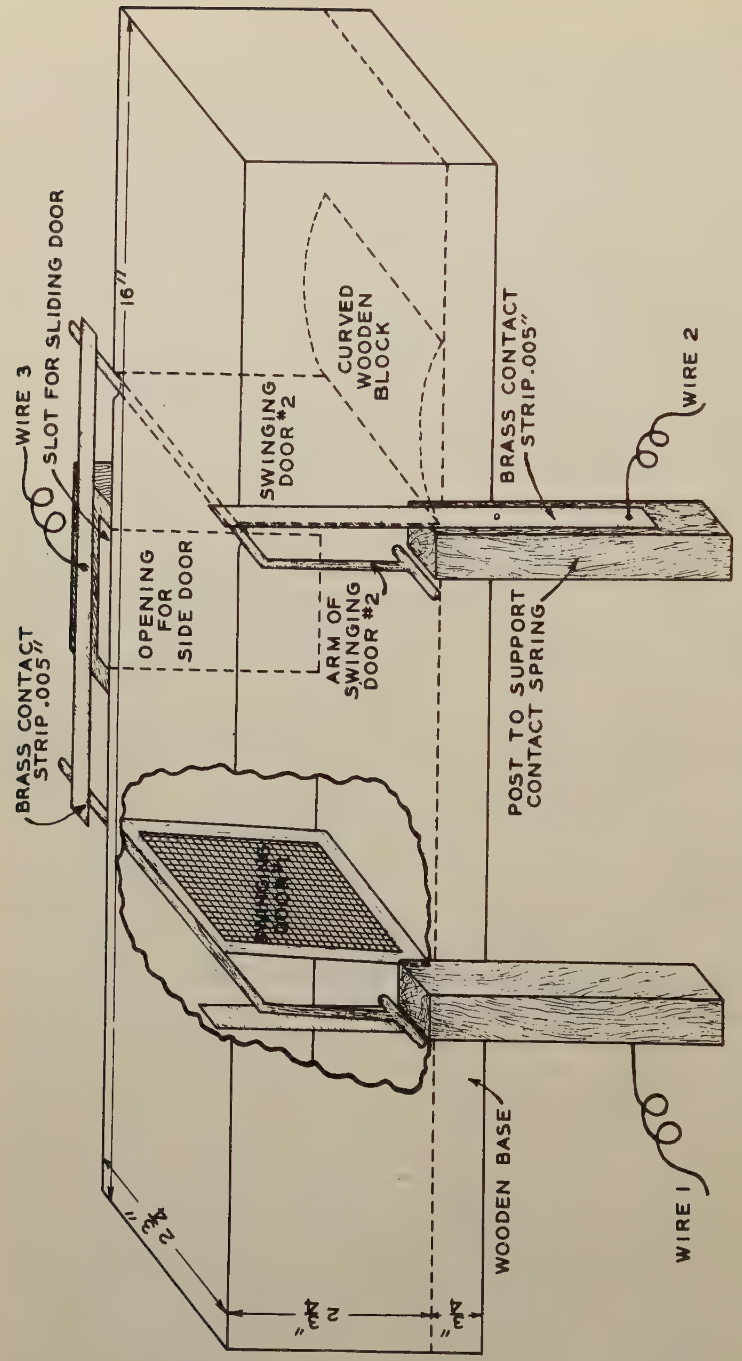


FIG. 1. Apparatus installed in the runway between the 2 compartments to record, in connection with a kymograph, the length of time the mouse remained in each compartment.

electromagnet, with the result that the horizontal arm of the recording apparatus changed its position, and the passage of the mouse was indicated.

The lines drawn by the kymograph pen attached to the end of the horizontal arm of the recording apparatus were at either of 2 horizontal levels. The upper position indicated that the mouse was in the north compartment, while the lower position indicated that the mouse was in the south compartment. The length of the line at either position, therefore, indicated the amount of time the mouse had spent in the corresponding compartment. As already explained, the position of the pen did not change until the mouse had crossed the runway and had opened the door to the compartment he was entering. If he came to the middle of the runway and then turned back, no change was made in the position of the recording pen.

The curved wooden blocks (Fig. 1) at each end of the horizontal runway forced the mouse to open the doors wide in order to pass through, and they thus insured a good electrical contact between the arm of the door and the brass strip.

The kymograph was driven by a synchronous electric motor, and its speed was reduced by 2 reducing gears to a rate which varied in the several experiments between 1 and 2 mm. per minute. The motor was started and stopped by an electric time clock which was adjusted to synchronize with the 12-hour night period in the reaction room.

Experimental Procedure

Insofar as possible, a definite procedure was followed in carrying out the experiments. Occasionally, events prevented strict adherence to this procedure, but deviations were allowed only if they seemed to be of little importance.

Conditions in the 2 compartments were kept as nearly equal as possible except for the habitat factor which was being tested. Essentially the same arrangement and distribution of the tufts of artificial grass and of the units of jungle were retained in all the experiments. For Experiment VII and subsequent experiments the distribution of the tree trunks was changed somewhat to a more regular pattern than that used in the earlier experiments.

Almost all of the mice were given a training period in order to acquaint them with the swinging doors and the activity wheels. The training periods were usually of 4 days' duration and always immediately preceded the testing period. Whether or not this training period increased the efficiency of the experiments is not known.

Training was accomplished in 2 ordinary laboratory cages connected by a runway which contained a swinging door like those in the experimental apparatus. One cage was provided with nesting material and water and the other with food and an activity wheel. This arrangement compelled the mice to pass through the runway to get the necessary food and water and a hiding place.

The first introduction of each mouse to the experimental situation was made by means of an introduction box (Pl. I, Fig. 1). This box was completely enclosed and admitted light only through a small screen door 2 by 2 1/2 inches. The door was hinged at its top and was so constructed that it could be pushed open from the inside but not from the outside. The box was placed on the partition of the reaction room and was connected with the side door of the runway apparatus by means of a screen-wire runway. After the first night of each mouse's test period, the introduction box was removed from the room.

Each mouse was tested for 4 consecutive nights. Records of the several measurements of habitat selection were taken daily in the early afternoon. This required the investigator to be present in the room for a half-hour to an hour. In general, the mice were not active during the daylight period unless disturbed by the record taking. The disturbance caused by record taking and by changing used nest boxes sometimes caused a mouse to run from compartment to compartment. A disturbed mouse was always allowed to remain wherever it was when the investigator left the room. There is no evidence that this disturbance had an effect on habitat selection in the experiments.

After each mouse was tested, the sand on the floor of the compartments was mixed and smoothed with a brush, and the activity wheels, nest boxes, food dishes, and water tubes and racks were washed in water. Between experiments the sand was sifted to remove mouse droppings and other debris. A clean nest box was substituted each day for the one used by the mouse, and the activity wheels were interchanged daily so that a particular wheel was placed in each compartment on alternate nights. Artificial habitats were changed from one compartment to the other at least once during each experiment following Experiment III. The significance of these procedures will be discussed below.

To maintain as nearly natural conditions as possible, the time clock was set to give approximately a 12-hour period of bright light and a similar period of dim light or darkness. Two 200-watt bulbs in each compartment supplied illumination during the period of bright light, which lasted approximately from 7:00 A.M. to 7:00 P.M. Dim light, when provided during the "night," was given by a 7-watt frosted bulb in the central light fixture of each compartment. A single sheet of typewriter paper covered the opening of each fixture. The illumination thus provided approximated 0.01 foot-candle when read on the floor directly beneath the light. This illumination is of about half the intensity of the light given by the zenithal full moon (Smithsonian Instit., 1918:218). The values varied somewhat from this figure, depending on the age of the bulbs and the voltage of the current. The light intensities were measured with a Weston Illumination Meter, Model 603, in the manner described by Dice (1945).

Occasionally one of the electric-light bulbs in the room burned out during an experiment. A single 200-watt bulb was discovered to be out on 9 different days during the experiments. The records show that this possibly caused an effect in the case of only 2 of 9 mice involved, both in Experiment V. Seven-watt bulbs burned out twice in the experiments, apparently without causing any effect on the reaction of the mice to the artificial habitats.

For habitat selection to occur in these experiments, it was necessary that the animal be acquainted with the alternatives to be selected. Almost all of the mice entered both compartments during the first night of their tests. If a particular mouse did not do this, a basis for habitat selection did not exist, and the data secured from that mouse were not used. Mice that did not enter both compartments during the first night of testing were not used again in any experiment.

Experimental Animals

Peromyscus maniculatus, the species studied in these experiments, ranges over most of North America from the limits of tree growth in Canada southward into southern Mexico and from the Atlantic to the Pacific Coast (Osgood, 1909). Subspecies of P. maniculatus live in many habitats within this range. The races gracilis and bairdi are excellent experimental animals for a study of habitat selection, since they show contrasting habitat preferences.

P. m. bairdi, the prairie deermouse, inhabits prairies, open fields, and lake beaches, as numerous ecological surveys have established (Wood, 1910; Dice, 1925). It is closely limited to open habitats and is rarely caught in woodland or in brushland (Wood, 1910; Blair, 1940). By extensive trapping in cultivated fields in central Missouri, I found that the catch of prairie deermice diminished to zero as the trap lines approached woody or brushy field borders. Yet this subspecies has been known to live in fields surrounded by woods, where it must presumably have passed through the woods in its dispersal movements (Howard, 1949).

The typical habitat of P. m. gracilis is the northeastern hardwood forest (Hooper, 1942), but it is also found in shrubby areas (Dice and Sherman, 1922) and in forest plantations where the trees are widely spaced and only a few feet tall (unpublished records of the author). It is thus apparently somewhat less strictly limited to the forest habitat than is the prairie deermouse to open fields.

As a consequence of deforestation and land cultivation, the prairie deermouse has extended its range eastward and northeastward (Hooper, 1942). It has thereby come into contact at some places with the forest deermouse. Both races occurred in one part of Charlevoix County, Michigan, without any evidence of intergradation (Dice, 1931a). In the laboratory, however, they will interbreed, and their F_1 hybrids of both sexes are fertile (Dice, 1933).

The mice used in these experiments were taken from the stocks of the Laboratory of Vertebrate Biology. In the laboratory they were given the same care received by all the mice (Dice, 1929). The P. m. bairdi stock, called Washtenaw in the laboratory records, was reared from individuals caught in fields about 3 miles west of the University. Some of the original field-caught individuals were tested in the first 3 experiments, but laboratory-born stock was employed in the remaining experiments. The field-caught P. m. gracilis specimens were obtained from a wooded area 1 mile east of Munising, Michigan. These are recorded as the Cusino stock in the laboratory but were later added to the Pine Lake stock of gracilis. The Pine Lake stock was reared from mice obtained in 1940 from the Cusino Wildlife Refuge, Munising, Michigan.

Although it was not possible to select mice of exactly the same age, only sexually mature and apparently normal individuals were used. Among the laboratory-bred mice the oldest mouse tested was 84 weeks of age and the youngest was 22 weeks old. Most were between 7 and 19 months. The ages of the field-caught individuals used in part of the first 3 experiments were, of course, unknown.

STATISTICAL ANALYSIS

The time required to test each mouse limited the number of mice that could be tested in a single experiment. Approximately 8 individuals of each race were tested in every experiment except those in which a clear-cut difference in artificial-habitat selection was apparent with fewer individuals.

The data are analyzed statistically by 2 methods. (1) Analysis of variance which employs the F test of significance (Snedecor, 1946:218) was used to evaluate the data for habitat selection as measured by the numbers of turns of the activity wheels, numbers of seeds eaten, and amounts of water consumed. (2) Comparison of means by the t test of significance (Snedecor, 1946:42) was employed to analyze the measurement of time spent in the artificial habitats.

Analysis of Variance

For the analysis of variance the data for each measurement were fitted to a 2 by 4 by n table which permitted comparison with the experimental error (F) of variations between the 2 habitats, of variations among the 4 days for the same mouse, and of variations among n mice. The significance of interactions between any 2 of these variations was also computed in the analysis. Whenever these interactions were not statistically significant, they were combined with the experimental error. The new F values derived are presented in the tables. Interactions between individual mice and days and between habitats and days were often combined with experimental error in the calculations.

It has already been explained that the count of seeds eaten was a close estimate and not a precise count. Estimated data may be analyzed statistically in the same way as exact data if the method of estimation does not bias the collection of the data. The results of statistical analysis for estimated data are no more accurate than the data.

Certain special cases pertaining to the calculation of the data by analysis of variance should be mentioned. A male P. m. bairdi was accidentally killed on the third day of observation in Experiment IV. The records for the fourth night were estimated by the formula for estimation of missing values. Another special case concerns the recording of certain data when observations were not made on 1 day. The amount of water supplied the mice in each habitat and the possible number of revolutions which could be recorded on the counter of an activity wheel were large enough not to be exceeded by the amount of water used or the number of turns on the wheel made by a mouse during a 2-day period. Rather than omit the data and replace it by estimation, readings were divided equally between those 2 days. This was done for 1 mouse in each of the following cases: bairdi, Experiment IV, wheel and water, second and third days; gracilis, Experiment VI, water, third and fourth days; and bairdi, Experiment VI, water, third and fourth days.

Items of data were occasionally not recorded because of oversight or conditions which prevented their being obtained. In order to use analysis of variance in a 3-way table, it is necessary to supply the missing table entries. A theory for the estimation of missing data has been developed (Goulden, 1939:261; Cochran and Cox, 1950:72), but the particular application needed here was not readily available. According to this theory, estimates are derived which minimize the error sum of squares. One degree of freedom is subtracted from the degrees of freedom associated with the error sum of squares for each estimated missing value. Dr. C. C. Craig supplied the specific formula used in these calculations. Since a description of this formula (Harris, 1950) is rather involved and applies only to the specific experimental design used here, it will not be repeated.

The data for numbers of seeds eaten and the amount of water consumed by males and females in each experiment were studied by analysis of variance to determine if a sexual difference in habitat selection occurred. The calculations were made separately for each of the 2 subspecies of Peromyscus. The daily records for each mouse in each artificial habitat were added, and the resulting values for one artificial habitat were subtracted from the corresponding values for the other artificial habitat. Thus, the reaction of each mouse to the 2 habitats was represented by a single value which was the difference between the 2 values for the 2 habitats in each experiment. The single values for male individuals in an experiment were then compared with the single values for the females by obtaining the ratio of variation between sexes to variation within sexes.

Comparison of Means

In the data for the amount of time spent in each of the 2 habitats, more than 5 missing table entries (a number arbitrarily chosen) sometimes occurred because of failure of the apparatus. As the number of missing values that must be supplied increases, the precision of the analysis of variance decreases. Another method of analysis, therefore, was advisable for the measure of time.

The number of minutes spent by a mouse in one habitat was directly related to the number of minutes spent in the other habitat.

Thus, the method used here is adapted to small samples in which values are paired and correlated (Smith and Duncan, 1945:403). The number of minutes spent each night by the mice in one habitat was subtracted from the number of minutes spent in the other habitat, and a t test of the difference of the subtracted values from zero was obtained. If there were no difference between the times spent by the mice in the 2 habitats, the total of the subtracted values would equal zero. It is to be noted that variation among daily records of each mouse was lost in this method of analysis. Each daily record was treated as though it were obtained from a different mouse. By eliminating variation among daily records of each mouse, this method of analysis becomes less precise than the method employed for the other measurements of habitat selection.

The correction of certain inaccuracies in the time record should be noted since they involve the data which are treated statistically. The period during which each nightly record was taken was regulated by time clock, and the lengths of the lines produced on the kymograph paper during these periods should always have been the same. Actually, they varied by several millimeters from day to day. This variation was eliminated by converting the time record from millimeters to minutes, the length of each day's line forming the basis of the conversion factor for that day. In this way the proportion of time spent by a mouse in each habitat and the total amount of time recorded each day were retained.

From the description of the runway apparatus it is evident that in certain circumstances an exact record of the time spent by a mouse in each habitat may not have been obtained. A mouse, after being in 1 habitat, could return to the center of the runway apparatus between the doors and remain there while still being recorded as present in the habitat which it had just left. This could also occur at the beginning and end of the mouse's activity periods during each night. These possible errors are assumed to be randomized between habitats and among the mice in each experiment.

When a mouse was released into the introduction box at the beginning of its 4-day testing period, the horizontal arm of the recording apparatus was placed halfway between the magnets. If the mouse did not become active until after the kymograph began to operate, a known period of time occurred during which the mouse was in neither artificial habitat. Similar periods of time could occur at the beginning and end of each of the other 3 nights as described in the preceding paragraph, but their occurrence and length were unknown. To omit the known period during which the mouse was inactive would again introduce a variation in the time record. For this reason the known period of time during which the mouse was in neither habitat at the beginning of the first night was divided between the habitats in the same proportion that occurred for the active part of the night.

DESCRIPTIONS AND RESULTS OF THE EXPERIMENTS

Descriptions of the precise conditions for each experiment, together with the results, are given here. The term "significant" in this section refers to significance in the statistical sense. The initials "d.f." signify degrees of freedom. The original data of these experiments and the tables recording the complete analyses of variance are given in the microfilm publication (Harris, 1950).

Experiment I

The reactions of the 2 subspecies of deermice, Peromyscus maniculatus gracilis and P. m. bairdi, to the tree-trunk and to the artificial-grass habitats were tested in this experiment. Cardboard disks were fastened to the tops of the tree trunks to produce shade simulating that caused by the foliage of natural trees. The tufts of artificial grass, 142 in number, were spaced 5 inches apart on the laths. Dim lights (approximately 0.01 foot-candles) produced illumination during the night period. A Petri dish containing 40 sunflower seeds was placed in each compartment. The artificial habitats were not changed from one compartment to the other during the experiment. Since guards were not present around the entrance to the horizontal section of the runway, it was possible for mice to go from compartment to compartment without passing through the section of the runway carrying the contact mechanism. A few gracilis did jump from the slanting part of the runway to the divisional wall and from there climbed to various nooks and crannies above the floor of the room.

Six male and 2 female bairdi and 4 male and 4 female gracilis were tested. All except 1 male bairdi and 2 male gracilis were field caught.

The F values computed by analysis of variance for 3 of the 4 measurements of habitat selection in this experiment are given in Table I. Total values for all 4 measurements are found in Table II. The difference between the mean times spent in the 2 artificial

TABLE I

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus gracilis and P. m. bairdi in Experiment I.

Source of Variation	Numbers of Revolutions Made in Activity Wheels		Numbers of Seeds Eaten		Milliliters of Water Consumed	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
Among individuals	4.41** (7;45)†	7.05** (7;43)	4.09** (7;42)	1.29 (7;43)	3.08* (7;43)	0.69 (7;43)
Between habitats	4.66* (1;45)	1.38 (1;43)	3.29 (1;42)	8.01** (1;43)	138.27** (1;43)	0.17 (1;43)
Among days	1.18 (3;45)	3.15* (3;43)	2.25 (3;42)	1.44 (3;43)	0.88 (3;43)	2.15 (3;43)
Interaction: habitats x individuals	2.09 (7;45)	10.31** (7;43)	7.73** (7;42)	2.93* (7;43)	14.38** (7;43)	5.54** (7;43)

*Value is significant at the 5 per cent level.
**Value is significant at the 1 per cent level.
† n_1 degrees of freedom; n_2 degrees of freedom.

TABLE II

Summary of Selection by Peromyscus maniculatus gracilis and P. m. bairdi Between Tree-trunk and Artificial-grass Habitats in Experiment I. Values are estimated for 11 items of missing data.

	8 gracilis		8 bairdi	
	Tree	Grass	Tree	Grass
Presence in habitat				
Total minutes	11353††	9227	5554	9146†
Per cent	55.2††	44.8	37.8	62.2†
Activity wheels				
Total turns	106701†	29171	103281	65822
Per cent.	78.5†	21.5	61.1	38.9
Seeds eaten				
Total seeds	621	511	342	558††
Per cent.	54.9	45.1	38.0	62.0††
Water consumed				
Total ml.	65.8††	17.9	35.6	33.2
Per cent	78.6††	21.4	51.7	48.3

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

habitats by gracilis is significant at the 1 per cent level (t = 11.00 with 27 d.f.), and by bairdi is significant at the 5 per cent level (t = 2.53 with 19 d.f.).

P. m. gracilis scored higher total values in the tree-trunk habitat than in the artificial-grass habitat in all 4 measurements of habitat selection. The tendency of gracilis to select the tree-trunk habitat is indicated by the significant difference between the 2 habitat means in each of 3 measurements: time, activity wheel, and water.

For bairdi, higher total values were obtained in the artificial-grass habitat than in the tree-trunk habitat in 2 of the 4 measurements of habitat selection. Significant differences between habitat means in these 2 measurements — time and seeds — show a tendency for bairdi to prefer the artificial-grass habitat.

In Experiment I, however, 2 variables were present: (1) Artificial habitats composed of tree trunks and of artificial grass presented vegetational differences. (2) The intensity of light differed on the floors of the compartments beneath the 2 artificial types of vegetation. This was true because the cardboard disks on the tree trunks produced more shade than the narrow strips of paper forming the artificial grass, so that, in general, the floor of the tree-trunk compartment was darker than that of the artificial-grass compartment.

Experiments II and III

Experiments II and III were designed to determine if light intensity affected artificial-habitat selection. The artificial habitats in these 2 experiments were the same as those in Experiment I. In Experiment II the intensity of the night light in the artificial-grass compartment was lowered from approximately 0.01 foot-candle to 0.0042 foot-candle by placing 4 sheets of typewriter paper over the opening of the central light fixture. Two male and 1 female gracilis and 3 male bairdi were tested. All had been previously used in Experiment I.

In Experiment III the night light in the tree-trunk compartment was reduced to 0.0038 foot-candle by 4 sheets of typewriter paper. A burlap curtain was dropped above the partition to further differentiate the intensities of light on the floors of the 2 compartments. It should be mentioned that the curtain interfered with air circulation and produced a difference in temperature of as much as 8^{0} F. between the 2 compartments, the tree-trunk compartment being the cooler. Three male gracilis and 3 male bairdi were tested. All except 1 male bairdi had previously been used in Experiments I or II or in both.

The data from these experiments were not treated statistically. In spite of the few mice tested, the gross results seem to indicate that light intensity may have been a factor influencing selection of the artificial habitats. The preference for the artificial-grass habitat shown by bairdi appeared to be strengthened, as compared with Experiment I, when the light intensity in the artificial-grass compartment was reduced, and was weakened when the light intensity of the tree-trunk compartment was reduced. A preference for the artificial-grass habitat was indicated by gracilis in the measurements of total time and activity-wheel turns when the light intensity was reduced in the artificial-grass compartment, and a weaker selection of the tree-trunk habitat was indicated by the measurements of seeds eaten and water drunk. The preference for tree trunks exhibited by gracilis seemed to be strengthened somewhat when the light intensity in the tree-trunk compartment was reduced.

Experiment IV

Light intensity on the floor beneath the artificial vegetation proved very difficult to measure precisely, and no adequate control of it could be devised. This factor was eliminated in Experiment IV by using no lights at all during the night period.

Since the cardboard disks now served no function, they were removed from the tree trunks. Tree-trunk and artificial-grass habitats were arranged as in the preceding experiments, and each was changed once from one compartment to the other during the experiment. Four male and 3 female gracilis and 3 male and 4 female bairdi were tested. All of these mice were laboratory bred and none had been previously tested.

The F values obtained from the analysis of variance of 3 measurements of habitat selection in Experiment IV are given in Table III. The totals of values obtained in all the measurements are recorded by habitat in Table IV. No significant difference occurred between the mean times spent by gracilis in the 2 artificial habitats ($t = 0.68$ with 20 d.f.). More time was spent by bairdi in the artificial-grass habitat, and the difference between mean times was significant at the 1 per cent level ($t = 9.65$ with 20 d.f.).

Values obtained in the tree-trunk habitat for gracilis were

TABLE III

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus gracilis and P. m. bairdi in Experiment IV.

Source of Variation	Numbers of Revolutions Made in Activity Wheels		Numbers of Seeds Eaten		Milliliters of Water Consumed	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
Among individuals	11.49** (6;39)†	10.73** (6;20)	1.19 (6;39)	1.45 (5;28)	0.55 (6;39)	5.05** (6;39)
Between habitats	4.70* (1;39)	5.79* (1;20)	25.70** (1;39)	64.97** (1;28)	188.36** (1;39)	122.00** (1;39)
Among days	0.82 (3;39)	3.68* (3;20)	0.16 (3;39)	0.09 (3;28)	0.30 (3;39)	0.61 (3;39)
Interaction: habitats x individuals	4.20** (6;39)	5.86** (6;20)	4.68** (6;39)	4.59** (5;28)	5.64** (6;39)	6.52** (6;39)
Interaction: days x individuals ..	....	2.33* (18;20)	.....	....	....	....

*Value is significant at the 5 per cent level.

**Value is significant at the 1 per cent level.

† n_1 d.f.; n_2 d.f.

TABLE IV

Summary of Selection by Peromyscus maniculatus gracilis and P.m. bairdi Between Tree-trunk and Artificial-grass Habitats in Experiment IV. Values are estimated for 6 items of missing data.

	7 gracilis		7 bairdi	
	Tree	Grass	Tree	Grass
Presence in habitat				
Total minutes ...	8297	7432	2219	13510††
Per cent.......	52.7	47.3	14.1	85.9††
Activity wheels				
Total turns	10936†	5896	37357	74234†
Per cent.......	65.0†	35.0	33.5	66.5†
Seeds eaten				
Total seeds	764††	409	199	686††
Per cent.......	65.1††	34.9	22.5	77.5††
Water consumed				
Total ml.	86.6††	27.6	23.8	82.0††
Per cent	75.8††	24.2	22.5	77.5††

† Represents a value significant at the 5 per cent level.

††Represents a value significant at the 1 per cent level.

greater than those obtained in the artificial-grass habitat, and the differences between mean values in the 2 habitats were significant in 3 measurements: wheel turns, seeds, and water. This indicates a preference for the tree-trunk habitat by gracilis. For bairdi differences between mean values in the 2 artificial habitats were significant in all 4 measurements. The greater of each pair of mean values was obtained in the artificial-grass habitat for each measurement, revealing the selection of that habitat by bairdi.

Experiment V

Habitat selection might theoretically occur either as a positive reaction toward certain features of the habitat selected or as a negative reaction against certain features of the habitat avoided. To gain information about these possibilities, in Experiment V the mice were offered habitats differing in only 1 feature of artificial vegetation. The tree-trunk habitat contained artificial grass in addition to the tree trunks, and it was contrasted with a habitat in which only artificial grass was present.

The arrangement of the tufts of artificial grass was closely similar in the 2 habitats; 98 tufts were used in the tree-trunk habitat and 102 tufts in the artificial-grass habitat. The tufts were spaced at 7-inch intervals on the laths in both compartments. Artificial habitats were changed from one compartment to the other once during the experiment. Dim lights were used during the night period since the intensity of light reaching the floor was nearly equal in the 2 compartments, differing only in the shadows cast by the tree trunks. Finger bowls for the sunflower seeds replaced the Petri dishes of previous experiments. Three male and 5 female gracilis and 4 male and 5 female bairdi were tested. None of these individuals had been tested in previous experiments.

In Tables V and VI, respectively, are found the F values for 3 measurements of artificial-habitat selection and the total values obtained for all measurements. The difference between mean times spent by gracilis in the 2 artificial habitats was significant at the 1 per cent level (t = 2.96 with 29 d.f.). There was no significant difference in the mean times spent by bairdi in the 2 habitats (t = 0.88 with 23 d.f.).

The tree-trunk and artificial-grass habitat was selected by gracilis in this experiment, as evidenced by the mean values which were higher in this habitat than in the artificial-grass habitat for all 4 measurements of habitat selection. The differences between

TABLE V

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus gracilis and P. m. bairdi in Experiment V.

Source of Variation	Numbers of Revolutions Made in Activity Wheels		Numbers of Seeds Eaten		Milliliters of Water Consumed	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
Among individuals	16.77** (7;21)†	2.87** (8;59)	0.59 (7;45)	1.21 (8;51)	0.71 (7;45)	1.54 (8;51)
Between habitats	0.10 (1;21)	5.66* (1;59)	18.51** (1;45)	5.88* (1;51)	15.74** (1;45)	3.11 (1;51)
Among days	2.00 (3;21)	2.43 (3;59)	0.06 (3;45)	0.61 (3;51)	1.23 (3;45)	1.06 (3;51)
Interaction: habitats x individuals	6.43** (7;21)	....	3.72** (7;45)	3.37** (8;51)	2.71* (7;45)	7.67** (8;51)
Interaction: days x individuals ...	2.36* (21;21)	....	....	....	....	....
Interaction: habitats x days	3.56* (3;21)	....	....	....	....	....

*Value is significant at the 5 per cent level.
**Value is significant at the 1 per cent level.
† n_1 d.f.; n_2 d.f.

TABLE VI

Summary of Selection by Peromyscus maniculatus gracilis and P. m. bairdi Between the Tree-trunk with Artificial-grass Habitat and the Artificial-grass Habitat in Experiment V.

	8 gracilis		9 bairdi	
	Tree + Grass	Grass Only	Tree + Grass	Grass Only
Presence in habitat				
Total minutes	14570††	7900	9977	12493
Per cent........	64.8††	35.2	44.4	55.6
Activity wheels				
Total turns	94183	87599	98893	198212†
Per cent	51.8	48.2	33.3	66.7†
Seeds eaten				
Total seeds	737††	358	439	642†
Per cent	67.3††	32.7	40.6	59.4†
Water consumed				
Total ml.	60.0††	35.0	42.4	53.2
Per cent	63.2††	36.8	44.4	55.6

†Represents a value significant at the 5 per cent level.
††Represents a value significant at the 1 per cent level.

mean values in the 2 habitats were significant at the 1 per cent level for 3 of the 4 measurements of habitat selection: time, seeds, and water.

No significant selection was made by bairdi for either of the 2 artificial habitats. Although the mean values obtained in the artificial-grass habitat were higher than those obtained in the tree-trunk and artificial-grass habitat, their differences were significant at the 5 per cent level for only 2 measurements: wheel turns and seeds. A considerable number of seeds in addition to those eaten was removed from the food dish and stored by the individuals of bairdi tested, and the mean values of seeds removed in the 2 habitats were not significantly different.

Experiment VI

In Experiment VI a jungle in one compartment opposed artificial grass in the other compartment. The jungle was arranged to cover the floor space almost completely, except for an aisle along 1 side of the compartment. The artificial-grass habitat remained as in previous experiments. No lights were used in the night period. During the experiment the artificial habitats were changed once from one compartment to the other. Five male and 3 female gracilis and 5 male and 3 female bairdi were tested. One female gracilis had been previously tested in Experiment V.

Aside from the form of the artificial vegetation, the tree-trunk habitat presented in these experiments 2 additional features that might be important in artificial-habitat selection. The floor of the tree-trunk compartment, as in Experiment IV, had little cover for the mice in comparison with that of the artificial-grass compartment. Also, the tree trunks themselves afforded an opportunity for gracilis to climb about, as it probably does in nature. These 2 features, in the absence of tree trunks, were presented by the jungle which, in a highly stereotyped manner, simulated a brushy habitat.

Table VII presents the F values obtained in the statistical analysis of 3 measurements of artificial-habitat selection. The total values for all 4 measurements are given in Table VIII. There was no significant difference between mean times spent by gracilis in the 2 artificial habitats ($t = 0.39$ with 30 d.f.). The mean time spent by bairdi in the artificial-grass habitat was significantly greater at the 1 per cent level ($t = 3.31$ with 30 d.f.) than that spent in the jungle habitat.

TABLE VII

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus gracilis and P. m. bairdi in Experiment VI.

Source of Variation	Numbers of Revolutions Made in Activity Wheels		Numbers of Seeds Eaten		Milliliters of Water Consumed	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
Among individuals	8.29** (7;43)†	4.52** (7;45)	1.65 (7;43)	4.45** (7;40)	2.72* (7;45)	1.10 (7;45)
Between habitats	1.26 (1;43)	0.43 (1;45)	17.36** (1;43)	16.07** (1;40)	1.56 (1;45)	10.74** (1;45)
Among days	0.56 (3;43)	0.83 (3;45)	1.01 (3;43)	0.62 (3;40)	0.26 (3;45)	1.50 (3;45)
Interaction: habitats x individuals	1.87 (7;43)	5.80** (7;45)	12.15** (7;43)	7.04** (7;40)	3.90** (7;45)	4.76** (7;45)

*Value is significant at the 5 per cent level.
**Value is significant at the 1 per cent level.
†n_1 d.f.; n_2 d.f.

TABLE VIII

Summary of Selection by Peromyscus maniculatus gracilis and P. m. bairdi Between Jungle and Artificial-grass habitats in Experiment VI. Values are estimated for 9 items of missing data.

	8 gracilis		8 bairdi	
	Jungle	Grass	Jungle	Grass
Presence in habitat				
Total minutes	11231	11988	8345	14874††
Per cent.	48.4	51.6	35.9	64.1††
Activity wheels				
Total turns	61025	32842	63021	79047
Per cent	65.0	35.0	44.4	55.6
Seeds eaten				
Total seeds	867††	577	323	606††
Per cent.	60.0††	40.0	34.8	65.2††
Water consumed				
Total ml.	61.6	53.6	35.0	52.0††
Per cent.	53.5	46.5	40.2	59.8††

††Represents a value significant at the 1 per cent level.

In this experiment no definite preference was shown by gracilis for either artificial habitat. Higher mean values were obtained in the jungle habitat than in the artificial grass for 3 measurements: wheel turns, seeds, and water. The differences between mean values in the 2 habitats were significant only for seeds eaten.

On the other hand, bairdi showed a preference for the artificial-grass habitat. This preference was manifested by higher mean values in the artificial-grass than in the jungle habitat for all 4 measurements. The differences between mean values of the 2 habitats were significant at the 1 per cent level for 3 of the measurements: time, seeds, and water.

Experiments VII and IX

As a crucial test for the positive selection of tree trunks by gracilis, tree trunks were contrasted with jungle as the artificial habitats used in Experiment VII. The tree trunks and jungle were arranged in the 2 compartments as in previous experiments. No lights were used during the night period. In this and the following experiments 45 sunflower seeds were placed daily in each food dish. The habitats were changed from compartment to compartment after each 2 mice were tested. Four male and 4 female gracilis were used; of these, 2 males and 2 females had been tested in previous experiments.

Experiment IX repeated Experiment VII, testing 3 male and 3 female gracilis, all but one of which were individuals not tested in Experiment VII. In Experiment IX the ventilating fan at one end of the room was turned off. Heat was provided by an electric heater with a circulating fan which was placed over one end of the partition. An electric fan was placed on the other end of the partition to aid in the circulation of warm air. The air currents produced by the fans caused no movement of the artificial grass.

The results of statistical analysis of 3 measurements of habitat selection in Experiments VII and IX are given as F values in Table IX. In Table X are recorded by habitat the total values of all 4 measurements in the 2 experiments. Differences between mean times spent by gracilis in the 2 artificial habitats were not significant in either experiment ($t = 1.00$ with 31 d.f. for Experiment VII and $t = 0.91$ with 21 d.f. for Experiment IX).

In Experiment VII a tendency was shown by gracilis to choose the jungle habitat in preference to the tree-trunk habitat.

TABLE IX

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus gracilis in Experiment VII and in Experiment IX.

Source of Variation	Numbers of Revolutions Made in Activity Wheels		Numbers of Seeds Eaten		Milliliters of Water Consumed	
	VII	IX	VII	IX	VII	IX
Among individuals	12.23** (7;20)†	5.03** (5;31)	1.74 (7;45)	1.82 (5;31)	1.17 (7;45)	3.59* (5;33)
Between habitats	8.23** (1.20)	0.67 (1;31)	14.89** (1;45)	1.16 (1;31)	12.81** (1;45)	0.03 (1;33)
Among days	0.63 (3;20)	1.64 (3;31)	0.21 (3;45)	0.09 (3;31)	0.79 (3;45)	0.21 (3;33)
Interaction: habitats x individuals	5.46** (7;20)	0.56 (5;31)	10.27** (7;45)	1.10 (5;31)	3.91** (7;45)	4.44** (5;33)
Interaction: days x individuals . . .	3.57** (21;20)	. . . .	. . . .	. . . .	. . . .	. . . .

*Value is significant at the 5 per cent level.
**Value is significant at the 1 per cent level.
† n_1 d.f.; n_2 d.f.

TABLE X

Summary of Selection Between Jungle and Tree-trunk Habitats by 8 Peromyscus maniculatus gracilis in Experiment VII and by 6 P. m. gracilis in Experiment IX. Values are estimated for 4 items of missing data in each experiment.

	Experiment VII		Experiment IX	
	Tree	Jungle	Tree	Jungle
Presence in habitat				
Total minutes	11024	12944	8851	7627
Per cent.	46.0	54.0	53.7	46.3
Activity wheels				
Total turns	31696††	14502	30338	32496
Per cent	68.6††	31.4	48.3	51.7
Seeds eaten				
Total seeds	549	815††	401	458
Per cent	40.2	59.8††	46.7	53.3
Water consumed				
Total ml.	57.4	83.8††	48.6	47.8
Per cent.	40.7	59.3††	50.4	49.6

†† Represents a value significant at the 1 per cent level.

The mean values obtained in the jungle habitat were higher than those obtained in the tree-trunk habitat for 3 measurements, and the differences between mean values of the 2 habitats were significant at the 1 per cent level for 2 measurements, seeds and water. For the fourth measurement, wheel turns, the higher value of the 2 occurred in the tree-trunk habitat, and the difference between means was significant at the 1 per cent level. In Experiment IX, however, with somewhat different but more equal experimental conditions, no significant selection was exhibited by gracilis. The total values in the 2 habitats for each measurement were close to equality, and the higher of the 2 habitat values occurred in the tree-trunk habitat for 2 measurements and in the jungle for the other 2 measurements.

Experiment VIII

It is evident from Experiment IV, in which no lights were present during the night period, that habitat selection by gracilis and by bairdi occurs in the absence of visual stimuli. Experiment VIII was designed to test the hypothesis that perception of the artificial habitat may be received through the vibrissae. Three male and 1 female gracilis and 3 male and 3 female bairdi were tested. Of these mice, a male gracilis and a male and a female bairdi had not been tested in previous experiments. If vibrissae are the sensory structures largely used in the selection of habitat, their removal from animals already tested would provide a crucial test. The mice were given the usual 4-day period of training. Each mouse was then etherized and the vibrissae were clipped close to the skin. After the mouse had fully recovered from the ether, it was released in the introduction box.

The artificial habitats presented for selection by the mice were tree trunks in one compartment and artificial grass in the other. Individual mice of the 2 subspecies were not tested alternately. Artificial habitats were changed from one compartment to the other once for each subspecies. As in Experiment IX, accessory fans were used in place of the one built into the air duct of the reaction room.

In Table XI are recorded the F values computed by analysis of the data obtained for 3 measurements of habitat selection. Table XII presents the total values by habitat for all 4 measurements. The difference between the mean values of time spent by gracilis in the 2 artificial habitats is significant at the 1 per cent

TABLE XI

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus gracilis and P. m. bairdi in Experiment VIII.

Source of Variation	Numbers of Revolutions Made in Activity Wheels		Numbers of Seeds Eaten		Milliliters of Water Consumed	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
Among individuals	8.13** (3;21)†	10.23** (5;33)	0.77 (3;18)	1.78 (5;33)	3.16* (3;21)	1.39 (5;33)
Between habitats	4.78* (1;21)	1.78 (1;33)	85.58** (1;18)	7.45** (1;33)	42.71** (1;21)	25.09** (1;33)
Among days	1.91 (3;21)	1.77 (3;33)	1.97 (3;18)	0.30 (3;33)	1.43 (3;21)	2.05 (3;33)
Interaction: habitats x individuals	5.21** (3;21)	6.79** (5;33)	3.84** (3;18)	2.83* (5;33)	6.73** (3;21)	12.46** (5;33)

*Value is significant at the 5 per cent level.
**Value is significant at the 1 per cent level.
†n_1 d.f.; n_2 d.f.

TABLE XII

Summary of Selection by Peromyscus maniculatus gracilis and P. m. bairdi Between Tree-trunk and Artificial-grass Habitats in Experiment VIII. The vibrissae of the mice had been artificially removed. Values are estimated for 3 items of missing data.

	4 gracilis		6 bairdi	
	Tree	Grass	Tree	Grass
Presence in habitat				
Total minutes....	8035††	3200	6846	9992
Per cent........	71.5††	28.5	39.4	60.6
Activity wheels				
Total turns	1555	3870†	43231	65815
Per cent........	28.7	71.3†	39.6	60.4
Seeds eaten				
Total seeds......	561††	139	277	454††
Per cent........	80.1††	19.9	37.9	62.1††
Water consumed				
Total ml.	52.0††	25.6	37.6	63.8††
Per cent	67.0††	33.0	37.1	62.9††

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

level (t = 5.19 with 14 d.f.). No significant difference occurred between the 2 mean values of time spent by bairdi in the 2 habitats (t = 1.94 with 21 d.f.).

The results of this experiment indicate that gracilis selected the tree-trunk habitat even though the individuals tested were deprived of their vibrissae. A significant difference at the 1 per cent level occurred between habitat means for 3 measurements — time, seeds, and water — with the higher of the 2 means for each measurement occurring in the tree-trunk habitat. For the measurement of activity-wheel turns the higher of the 2 habitat means occurred in the artificial-grass habitat, and the difference was significant at the 5 per cent level.

Vibrissaeless bairdi showed a tendency to select the artificial-grass habitat. Mean values obtained in this habitat were higher than those obtained in the tree-trunk habitat. For 2 measurements — seeds and water — the differences between habitat means were significant at the 1 per cent level. The selection of the artificial grass by vibrissaeless bairdi was not so strong as that by bairdi with vibrissae intact in Experiment IV.

Experiment X

Since bairdi and gracilis produce fertile offspring in the laboratory (Dice, 1933) but apparently do not do so in nature (Dice, 1931a), artificial-habitat selection by their F_1 hybrids might be expected to furnish interesting information. Four male and 3 female F_1 hybrids of a bairdi x gracilis cross were tested in Experiment X for their selection between tree trunks and artificial grass. All 3 females were pregnant at the time of testing. The ventilating fan of the reaction room was turned off. No night lights were used during the tests. The artificial habitats were changed twice from one compartment to the other during the experiment.

F values computed by analysis of variance for 3 measurements of habitat selection in Experiment X are presented in Table XIII. Total values recorded by habitats for all measurements are given in Table XIV. The difference between mean times spent by the hybrids in the 2 artificial habitats is significant at the 1 per cent level (t = 3.72 with 20 d.f.).

The F_1 hybrids of bairdi x gracilis selected the artificial-grass habitat. The means obtained in this habitat for all measurements of habitat selection were higher than those obtained in the tree-trunk habitat, and the differences between means in the 2

TABLE XIII

F Values for 3 Measurements of Habitat Selection by Peromyscus maniculatus bairdi x P. m. gracilis F_1 in Experiment X.

Source of Variation	Numbers of Revolutions Made in Activity Wheels	Numbers of Seeds Eaten	Milliliters of Water Consumed
Among individuals	4.98** (6;37)†	3.84** (6;45)	11.71** (6;36)
Between habitats	4.28* (1;37)	12.54** (1;45)	38.49** (1;36)
Among days	2.31 (3;37)	1.49 (3;45)	1.42 (3;36)
Interaction: habitats x individuals	2.72* (6;37)	. . . .	2.82* (6;36)
Interaction: days x habitats	. . . .	. . . .	7.56** (3;36)

*Value is significant at the 5 per cent level.
**Value is significant at the 1 per cent level.
† n_1 d.f.; n_2 d.f.

TABLE XIV

Summary of Selection by 7 Peromyscus maniculatus bairdi x P. m. gracilis F_1 Between Artificial-grass and Tree-trunk Habitats in Experiment X. Values are estimated for 4 items of missing data.

	Tree	Grass
Presence in habitat		
Total minutes	5057	10654††
Per cent.	32.3	67.7††
Activity wheels		
Total turns	49190	94545†
Per cent	34.2	65.8†
Seeds eaten		
Total seeds.	440	754††
Per cent	36.9	63.1††
Water consumed		
Total ml.	61.6	107.8††
Per cent.	36.4	63.6††

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

habitats were significant at the 1 per cent level for all measurements except activity-wheel turns. In the latter instance, significance occurred at the 5 per cent level.

Artificial Habitats Selected

When the experiments described above are considered as a whole, it is noted that each subspecies usually selected the artificial habitat which simulated its natural habitat.

P. m. gracilis, the forest deermouse, showed a definite preference for the tree trunks when this habitat opposed the artificial grass in Experiments I, IV, V, and VIII. This selection was indicated by the mean values of the 4 measurements of habitat selection which, with 1 exception, were higher in the tree-trunk habitat than in the artificial grass. In each of these experiments 3 of the 4 measurements exhibited statistically significant differences between habitat means. In all of these experiments statistical significance occurred in 13 of the 16 measurements. In 10 measurements differences between habitat means were significant at the 1 per cent level and in 3 measurements, at the 5 per cent level. Of the latter, the measurement of wheel turns constituted the exception in which the higher of the 2 habitat means was in the artificial grass (Table XV). In Experiment I the selection was somewhat weaker than in the other experiments, in that the difference between the numbers of seeds eaten in the 2 habitats was not statistically significant. In this experiment, however, dim lights during the night periods caused unequal intensities of illumination on the floor of the 2 compartments.

P. m. gracilis did not respond in a consistent manner when jungle was opposed either to tree trunks or to artificial grass. In Experiment VI a tendency was shown to select the jungle habitat rather than the artificial-grass habitat, but in only 1 measurement was this preference statistically significant (Table XV); therefore, this weak habitat preference is not convincing. Jungle was also used in Experiment VII, but in contrast with tree trunks. Here, gracilis showed a preference for jungle, but the records suggest that some other factor was also involved in the choice. This experiment was repeated, therefore, as Experiment IX in an attempt to eliminate possible differences between the compartments which may have existed in addition to the differences in the habitats. There was now no preference shown by gracilis either for the jungle or for the tree trunks.

TABLE XV

Summary of Selection by Peromyscus maniculatus gracilis Between Contrasting Artificial Habitats.

Experiment	Light Intensity in f.c.	Habitat with the Higher Mean			
		Total Time in Habitat	Activity-Wheel Turns	Seeds Eaten	Water Consumed
I Tree vs. grass	0.01	tree††	tree†	tree	tree††
IV Tree vs. grass	dark	tree	tree†	tree††	tree††
V Tree + grass vs. grass	0.01	tree††	tree	tree††	tree††
VI Jungle vs. grass	dark	grass	jungle	jungle††	jungle
VII Tree vs. jungle	dark	jungle	tree††	jungle††	jungle††
VIII Tree vs. grass: mice with vibrissae removed	dark	tree††	grass†	tree††	tree††
IX Tree vs. jungle: without ventilating fan	dark	tree	jungle	jungle	tree

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

TABLE XVI

Summary of Selection by Peromyscus maniculatus bairdi Between Contrasting Artificial Habitats.

Experiment	Light Intensity in f.c.	Habitat with the Higher Mean			
		Total Time in Habitat	Activity - Wheel Turns	Seeds Eaten	Water Consumed
I Tree vs. grass	0.01	grass†	tree	grass††	tree
IV Tree vs. grass	dark	grass††	grass†	grass††	grass††
V Tree + grass vs. grass	0.01	grass	grass†	grass†	grass
VI Jungle vs. grass	dark	grass††	grass	grass††	grass††
VIII Tree vs. grass: mice with vibrissae removed	dark	grass	grass	grass††	grass††

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

The results of these 3 experiments (VI, VII, and IX), when viewed together, indicate that gracilis made no consistent choice between the jungle and tree trunks or between the jungle and artificial grass. It is possible that the highly artificial nature of the jungle, which has no counterpart in natural vegetation, did not stimulate habitat selection by gracilis.

In Experiment V the tree trunks with artificial grass were selected by gracilis over the habitat with artificial grass alone (Table XV). Apparently, the presence of artificial grass together with the tree trunks did not modify the natural habitat selection for tree trunks by gracilis. Thus, it appears that attention was directed by gracilis to the tree trunks and that there was a positive selection for them. This interpretation, however, is not fully convincing in view of the lack of pronounced habitat preference shown by gracilis in Experiments VII and IX, in which the tree-trunk habitat was contrasted with jungle.

To consider only those experiments in which tree trunks and artificial grass were presented as the contrasting artificial habitats, it seems evident from the generally consistent and statistically significant results that gracilis preferred the tree-trunk habitat. There is some suggestion that this habitat selection is a positive reaction to the tree trunks, but this evidence is not completely consistent.

Table XVI shows that P. m. bairdi, the prairie deermouse, selected the artificial-grass habitat with a high degree of consistency when this was opposed either to the tree-trunk habitat or to the jungle (Experiments I, IV, VI, and VIII). The mean values resulting from the measurements were higher in the artificial grass than in the opposed habitats. Experiment I offers the only exception to this; the means obtained in the tree-trunk habitat were higher than those obtained in the contrasting artificial-grass habitat for activity-wheel turns and for water consumed. This was a preliminary experiment, however, in which the dim light used during the night period was a complicating factor.

Experiment IV, in which no light was used during the night period, was the crucial test for selection between tree-trunk and artificial-grass habitats. In this experiment bairdi selected the artificial-grass habitat as shown by significant differences between habitat means in all 4 measurements, 3 of them being significant at the 1 per cent level and 1 at the 5 per cent level. In all of these 4 experiments, in which artificial grass opposed either tree trunks or jungle, statistical significance occurred in 11 of the 16 measurements. Differences between habitat means were significant at the

1 per cent level for 9 measurements and at the 5 per cent for 2 measurements.

The nature of the selective process of bairdi is suggested by the results of Experiment V in which the artificial-grass habitat opposed tree trunks with artificial grass (Table XVI). The values of all 4 measurements were higher in the artificial-grass habitat than in the habitat composed of tree trunks and artificial grass, but significant differences between the habitat means occurred at the 5 per cent level for only 2 measurements, activity-wheel turns and seeds eaten. This result, in comparison with the results of Experiment IV in which the opposing tree trunks were not associated with artificial grass, suggests that bairdi was definitely attracted to artificial grass but that it avoided tree trunks to only a slight extent. The slight tendency to avoid tree trunks may account for the fact that bairdi in nature is not found even in those woodlands that have a grassy ground cover.

In summary, P. m. bairdi in these experiments selected artificial habitats containing objects having a grasslike form. The response to the artificial grass seemed to be mostly positive, but a slight negative response to tree trunks may also have been present.

The experiments described above give a small amount of evidence about the sensory nature of the stimulus received by the mice in making a selection of artificial habitats. In Experiment IV both subspecies selected artificial vegetation corresponding to their natural habitats, even when the reaction room was in darkness. Also, in Experiment VI bairdi made a clear-cut selection under the same condition of darkness. The general inactivity of the mice during the 12-hour period of bright light precludes the possibility that they could have learned the experimental situation and made a selection during that period. Thus, the selective process is able to operate independently of visual stimuli.

In an effort to learn if the stimulus resulting in artificial-habitat selection was a tactile one received through the vibrissae, the mice were tested in Experiment VIII after the vibrissae had been removed. Four individuals of vibrissaeless gracilis selected the tree-trunk habitat in darkness. Differences between habitat means were significant at the 1 per cent level for 3 of the 4 measurements (Table XV). A preference for the artificial grass by vibrissaeless bairdi was also obtained in this experiment. Differences between habitat means were significant at the 1 per cent level for seeds eaten and water consumed, the 2 best measures of habitat selection. For total time and for activity-wheel turns, higher means were obtained in the artificial-grass habitat than in the tree-trunk habitat, but the differences were not statistically significant (Table XVI).

Of the individuals tested in Experiment VIII, 3 gracilis and 4 bairdi had also been tested in previous experiments. It seems unlikely, however, that, if vibrissae are important in habitat selection, previous learning by these individuals could have been almost completely substituted for a definite dependence upon them. Vibrissae are apparently used to some extent by the mice, for I have observed individuals running along the walls of the compartment without bumping into them at the corners. On the other hand, when the mice were excited or frightened, they frequently bumped into objects in their paths. Further, a few bairdi with vibrissae intact gave much the same performance in a small obstacle course as the same number of bairdi with the vibrissae removed.

These results show, I believe, that neither vision nor the tactile organs of the vibrissae are the chief sensory agencies through which the stimuli used in habitat selection are received by the mice. The incidental observations mentioned above do not disagree with this conclusion. Sensations received through the feet, tail, and other parts of the body may be more important in habitat selection than either vision or the sensory function of the vibrissae. These experiments, however, were not designed for a study of sensory stimuli, and the results are to be regarded merely as suggestive.

The responses of males and females to artificial-habitat selection were examined by analysis of variance. A significant sex difference in habitat selection was present in only 1 measurement, that of seeds eaten by gracilis in Experiment IX. When the data for similar experiments were pooled, however, significant differences between sexes were sometimes indicated. Perhaps the differences were not significant in the analyses of single experiments because so few individuals of each sex were involved. As far as these experiments are concerned, it is possible, therefore, that sex differences in artificial-habitat selection may occur, but it seems unlikely that sexual selection of gross differences in habitat would characterize the behavior of these mice in nature.

No consideration has been given to possible seasonal changes in habitat selection inherent in the mice. This was not practical in the present investigation because of limitations of time and equipment. No suggestion was obtained, however, of any change in the habitat preference of the subspecies correlated with the progression of the outdoor seasons.

FACTORS WHICH MAY HAVE INFLUENCED RESULTS OF THE EXPERIMENTS

Factors other than artificial vegetation which may have influenced the responses of the mice in the experiments should be considered. The possibility that the mice may have selected or avoided one compartment or the other, rather than the artificial vegetation therein, must be examined. Such a possible selection or avoidance may have been due to some irrelevant factor connected with the compartment, as, for example, its position. To control these possible effects of position, the artificial habitats were changed from one compartment to the other at least once during each experiment following Experiment III.

TABLE XVII

Statistical Analysis of Habitat-selection Data Divided According to Compartment of the Reaction Room. Values of t and F are for differences between north and south compartments.

Experiment	t Values		F Values			
	Total Time in Compartment		Seeds Eaten in Compartment		Water Consumed in Compartment	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
IV Tree vs. grass	0.72	0.35	16.33**	0.00	1.34	3.20
V Tree + grass vs. grass	0.54	0.88	2.21	6.23*	0.63	13.42**
VI Jungle vs. grass	3.73**	2.06*	14.77*	16.21**	5.06*	2.26
VII Jungle vs. tree: ventilating fan at one end of room	1.74	....	16.98**	....	14.19**	....
VIII Tree vs. grass: mice with vibrissae removed	0.54	2.09*	2.41	6.63*	4.75*	6.18*
IX Jungle vs. tree: ventilating fan in middle of room	1.20	....	0.02	....	5.65*	....
X Tree vs. grass	bairdi x gracilis 0.98		bairdi x gracilis 2.91		bairdi x gracilis 8.47**	

* Value is significant at 5 per cent level.
** Value is significant at 1 per cent level.

To evaluate the effect of position, the data obtained for the measurements of total time, seeds eaten, and water consumed were tabulated by compartment rather than by artificial habitat and were statistically analyzed as already described. In this analysis differences appear between north and south compartments in place of differences between artificial habitats. The F and t values for differences between north and south compartments are set forth in Table XVII. Of the 2 compartments, the one showing the higher value for each experiment and for each measurement is indicated in Table XVIII. From Table XVIII it is seen that, although there is some consistency within an experiment for the compartment with the higher value, there is little consistency in this regard from experiment to experiment.

TABLE XVIII

Summary of Habitat-selection Data Divided According to Compartments of the Reaction Room. The compartment which has the higher of the 2 totals for each measurement is indicated.

Experiment	Total Time in Compartment		Seeds Eaten in Compartment		Water Consumed in Compartment	
	gracilis	bairdi	gracilis	bairdi	gracilis	bairdi
IV Tree vs. grass	north	south	north††	north	north	north
V Tree + grass vs. grass	north	north	north	north†	north	north††
VI Jungle vs. grass	south††	south†	south††	south††	south†	south
VII Jungle vs. tree: ventilating fan at one end of room	south	. . . .	south††	. . . .	south††	. . . .
VIII Tree vs. grass: mice with vibrissae removed	north	south†	north	south†	south†	north†
IX Jungle vs. tree: ventilating fan in middle of room	north	. . . .	north	. . . .	north†	. . . .
X Tree vs. grass	bairdi x gracilis south		bairdi x gracilis south		bairdi x gracilis south††	

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

In comparing Table XVII with the appropriate entry (variation between habitats) in each of Tables I, III, V, VII, IX, XI, and XIII, and with the text, it is noted that the F and t values are generally lower for differences between compartments than for differences between artificial habitats. This is especially true in those experiments where a definite selection for artificial habitat occurred (Experiments IV and VIII for both subspecies, V for gracilis, VI for bairdi, and X for the hybrids). Where no strong selection was manifested by Peromyscus, the F and t values for compartment differences were not so much lower or were somewhat higher than those for differences between artificial habitats. This suggests that, where a combination of artificial habitats did not stimulate selection by the mice, some other less important difference between the compartments received their attention.

Another factor may have complicated the analyses of the data for north and south compartments. The number of mice tested when a given habitat was in one compartment was not always the same as the number tested when that habitat was changed to the other compartment. For example, in an experiment 5 bairdi may have been tested when artificial grass was in the north compartment, but only 3 bairdi when it was in the south compartment. The evidence from the F and t values has indicated that the main difference between compartments was the artificial vegetation. If bairdi selected the artificial grass in the example given above, an analysis of north and south compartments would show favor to the north compartment since more mice were tested when artificial grass was present there and fewer mice when artificial grass was present in the south compartment. A qualitative analysis of the data seems to accord with this belief. Hence, the analysis for north and south compartments may show more difference between compartments than really existed.

The use of the introduction box, previously described, considerably reduced the chance that cues for selection might have been given by the experimenter when he entered the room through 1 compartment to release the mouse. Also, the mouse was free to turn in either direction upon entering the runway apparatus, and thus the first artificial habitat entered would presumably be a matter of chance. Most of the mice remained in the box until long after the experimenter left the room, but occasionally a nervous individual would leave almost instantly.

Preliminary studies revealed that many mice formed a habit of returning to the nest box first occupied during a test. An attempt to break this habit by substituting each day a clean nest box for the one previously used by a particular mouse was not completely successful. Lack of more complete success was apparently occasioned because the introduction box must often have represented the nest box first occupied. The mice first entered the reaction room from the introduction box, and some individuals returned each day to the area between the swinging doors of the runway, which was the closest approach to the introduction box. There is no evidence that nest-box habit influenced those activities of the mice which provided the measures of artificial-habitat selection.

Several procedures were employed to eliminate the possibility that odors left by a mouse influenced the behavior of any mouse tested later in the reaction room. In those experiments in which both subspecies were investigated (except in Experiment VIII), the subspecies were alternated, that is, a test for an individual of one subspecies would be followed by a test for an individual of the other subspecies. By this procedure it is believed that, if a scent pattern should be laid down in some manner by one subspecies, it would be nullified by that of the other subspecies. In the statistical sense this is an attempt to randomize the scent factor. It was occasionally impossible to adhere strictly to this procedure, sometimes because of the death of a mouse in the training cage, and sometimes because of failure of a mouse to enter both habitats during the first night. As another precaution, after the 4-night test period of each individual, the sand on the floor of the 2 compartments was mixed and smoothed with a brush. Also, after each mouse was tested, the activity wheels, nest boxes, food dishes, and water tubes and racks were washed in water. Between experiments the sand was sifted to remove mouse droppings and other debris. It may be doubted, therefore, that the habitat selection of a mouse was seriously influenced by the scent left by mice previously tested in the reaction room.

The reaction room in which the experiments were conducted is not soundproof. At one end of the room the ventilating fan made a continuous buzz during most of the experiments, while near the other end of the room the reducing gears of the recording apparatus could be heard through the wall. These and less regular sounds were randomized by exchanging the artificial habitats from compartment to compartment during the course of each experiment.

The temperature varied somewhat in different parts of the reaction room, partly because in winter warm air entered one end of the room and became cooled as it passed toward the outlet at the other end. Radiation of heat from the walls of the room also affected the temperature. The reaction room is situated in a corner of the building; 2 walls of the south compartment and 1 wall of the north compartment are outside walls. Less heat radiates from the outside walls; hence the south compartment was somewhat cooler than the north compartment. During warm periods of the year the air temperature near the floor varied about 2° F. from place to place in the room, but during cold weather it varied as much as 8° F. The effect of this temperature variation was randomized by reversal of the artificial habitats during each experiment.

Relative humidity in the reaction room was low during the winter owing to artificial heating of the building. It must have differed from place to place in the room at those times when a gradient of air temperature occurred. The possible differences between compartments in air humidity were randomized by changing the artificial habitats.

Air currents in the room are believed to have had no effect on the reactions of the mice. None of the air currents was of sufficient strength to cause any perceptible movement of the artificial grass.

The effect of light intensity on habitat selection has already been described in Experiments II and III. The preference for artificial grass and for tree trunks by bairdi and by gracilis, respectively, appeared to be less definite when the intensity of the night light was reduced in the unpreferred habitat than when it was reduced in the preferred habitat. Light intensity was controlled in all the experiments following Experiment III by equalizing the light intensities on the floors of the 2 compartments (Experiment V) or by using no lights during the 12-hour night period.

RELIABILITY AND VARIABILITY IN SELECTION OF ARTIFICIAL HABITATS

The experiments described demonstrate that the 2 deermouse subspecies, bairdi and gracilis, under controlled laboratory conditions usually selected different types of artificial habitat. P. m. bairdi, with very few exceptions, selected the artificial-grass habitat in all experiments, as indicated by each of the 4 measures of habitat selection. Similarly, gracilis, with few exceptions among the 4 measures, selected the tree-trunk habitat in those experiments in which tree trunks were contrasted with the artificial-grass habitat. It has been demonstrated further that the most important difference between the 2 compartments to which the mice responded was the artificial vegetation. It may be concluded, therefore, that the experimental technique was adequate to measure habitat selection. Similarly, the consistency with which the activities of eating, drinking, and, to a less extent, running in the activity wheel were pursued more by a particular subspecies in one type of habitat than in the other, together with general activity as measured by total time, indicates that these are valid measures of habitat selection.

In spite of the evidence that bairdi preferred the artificial grass and that gracilis preferred the tree trunks, neither form entirely avoided the opposite type of habitat in these experiments. A complete avoidance would not be expected in view of the small area of the reaction room as compared with the area of the individual home range of either race in nature. The average size of the home range of adult bairdi in nature, as determined by Blair (1940), is 0.63 acre for males and 0.51 acre for females, but Howard (1949) presented evidence for a home range of several acres. The size of the average home range of adult male gracilis is 2.31 acres and of adult female gracilis is 1.39 acres (Blair, 1942). The small area (.004 acre) of the reaction room would be expected to affect artificial-habitat selection by reducing its strength, but this did not occur to such an extent that selection could not be demonstrated. On the other hand, the areas of the 2 compartments were so small that a mouse could investigate all parts of each of them during the first night of testing and could then proceed to select between the 2 artificial habitats which they contained.

The analyses of variance of turns of the activity wheel, number of seeds eaten, and amount of water consumed demonstrate that, of the 6 sources of variation for each of these measures of habitat selection, differences between habitats and between habitat-individual interaction are most often statistically significant. Also, these 2 sources of variation show, in most cases, high F values. Usually the F values for habitat differences are higher than those for habitat-individual interactions. Thus, the sources of significant variation in the analyses of variance are differences between habitats and between habitat-individual interaction.

A significant interaction between habitat and individuals means that in an experiment different individuals react to habitat differences with significantly different degrees of strength, even though as a group all of the individuals in that experiment reacted significantly to 1 type of artificial habitat. It should be emphasized that in the statistical computations a significant difference in reaction to habitats is in no way affected by a significant individual-habitat interaction.

Variation among individuals is less often significant for each of the 3 measures of habitat selection in all the experiments than is variation between habitats or habitat-individual interaction. Of the 3 measures of habitat selection in which individuals show significant variation, wheel activity supplies almost two-thirds of the occurrences. The few instances of significance among the remaining sources of variation, that is, variation among days of a test, variation in habitat-day interaction, and variation in individual-day interaction, occurred with 1 exception (habitat-day interaction for water in Experiment X) for the measure of activity-wheel turns. The fact that these several sources of variation show statistical significance most often in turns of the activity wheel is due to the great variation in the use of the wheel by different mice. The studies by Dice and Hoslett (1950) of activity-wheel records of several laboratory stocks of Peromyscus demonstrate great variability among individuals.

Thus the analyses of variance of seeds eaten and of water consumed reveal that no great amount of statistically significant variation, other than variation between habitats and variation in habitat-individual interaction, exists in these experiments. The variation in turns of the activity wheel has been explained. Variation between habitats is characteristically more significant (higher F values) than is variation in habitat-individual interaction. The differential response of a subspecies to the artificial habitats is the significant variable in the experiments, and the measurement of this response is the object of this investigation.

The relative effectiveness of the several methods for measuring habitat selection may be estimated by the frequency with which the measurements reveal a statistically significant difference in artificial-habitat selection by the mice. If each experiment and each race and the hybrids of Peromyscus are considered separately, 13 occurrences of a statistically significant habitat selection were possible for each measure. A statistically significant habitat selection, as measured by the number of seeds eaten, occurred in 11 of the 13 possibilities; as measured by the amount of water consumed, in 9 of the 13 possibilities; as measured by the total time in each habitat, in 7 of the 13 possibilities; and as measured by the number of turns of the activity wheels, in 7 of the 13 possibilities. Accordingly, the number of seeds eaten and the amount of water drunk appear to be the best measures of artificial-habitat selection by the mice. Total time is a better measure than activity-wheel turns, since the latter, as explained above, showed considerable variability among individuals. Activity-wheel turns could have been eliminated as a measure of artificial-habitat selection.

An attempt was always made to use different mice in the experiments (except in Experiment VIII), but because of lack of breeding during winter in the gracilis stock not many new individuals of this subspecies were available for the later experiments. The purpose in avoiding repetition in the individuals tested was to prevent modification and change of artificial-habitat selection by the mice due to learning and remembering. The reactions to artificial habitats of 8 out of 9 mice that were tested more than once in different experiments can be compared. Four of these mice showed consistent selection of a particular habitat type, 2 showed inconsistent selection, and 2 reversed the habitat type selected. Also, 3 individuals were by error tested twice in Experiment V. One was consistent in habitat selection, 1 showed partial reversal, and 1 showed complete reversal in the habitat chosen. No corrections or eliminations were made in the statistical analyses for the individuals that were tested more than once. These few data do not give evidence that change in artificial-habitat selection by a mouse tested in different 4-day periods is due to learning and remembering. They do indicate that it is wise to avoid repeating tests of the same mouse in the same or in similar experiments.

It seems reasonable that learning would weaken artificial-habitat selection by increasing the variability of the response. Such an effect would have to occur in most cases within the 4-day test period of each mouse, and the statistical evidence indicates that variation in the response of the mice among days of the test period was, in general, due to chance. Furthermore, the results of most of the experiments show that selection did occur in spite of any learning that might have weakened it.

The laboratory cages in which the mice were born and lived may also have conditioned them in a way to modify their preference for a particular artificial habitat. If this happened, and it is not possible to determine whether or not it did, it would probably have weakened the effect of their selection.

There is no evidence that learning and habit formation reinforced instinctive habitat selection by the mice in the experiments. Undoubtedly, habit formation entered into the reaction of the mice to artificial habitats, and it is possible that it may have reduced the sharpness of the selection which occurred. The probability that learning occurred does not affect the conclusions with reference to artificial-habitat selection by Peromyscus in these experiments.

FACTORS SELECTED IN THE HABITAT

A number of ecologists have discussed the problem of habitat selection by animals (Shelford, 1911; Grinnell, 1917; Dice, 1931b; and others). Elton (1927: 39-41) treated the subject rather fully. He believed that most animals are limited in their distribution by their habits and reactions. Their reactions presumably are suited to their particular physiological requirements and to their breeding habits. The stimuli which cause this distributional limitation, presumably to the optimum conditions for their life, may not themselves be directly harmful to the animal; they probably are more in the nature of signs or cues, warning the animal that it is approaching less suitable conditions for life. Thus, the immediate causes of the limitation in distribution may often be found in the psychological reactions of the animal.

Factors Previously Suggested by Authors

Among the factors that have been previously suggested by various authors as controlling the habitat distribution of animals, meteorological factors, light intensity, food and water, nesting sites, and interspecific dominance merit particular attention.

Meteorological Factors. — The effect of the evaporating power of the air on the reactions of Peromyscus leucopus noveboracensis, a woodland and brush-inhabiting species, was studied by Chenoweth (1917). In his experiments the mice were free to choose between different evaporating powers of air in a gradient apparatus. He concluded that evaporation rate, whether produced by movement, dryness, or temperature of the air, is probably the most important factor in determining the habitat distribution of this species.

The quantity of water and food used by Peromyscus l. noveboracensis and P. maniculatus bairdi under different conditions of air temperature and humidity was studied by Dice (1922). His experiments did not show sufficient differences between the 2 species of Peromyscus in their requirements for food, water, temperature, and air humidity to explain their habitat differences. Thus, he did not substantiate Chenoweth's conclusion in regard to habitat selection by P. l. noveboracensis.

The effect of climatic conditions on these same 2 species of Peromyscus was studied by Johnson (1926). Principally by comparison of climatic records obtained in both field and woodland habitats, he concluded that climatic factors do not explain the restriction of the 2 species to their respective habitats. He believed that their habitat distribution depends upon the whole biotic association type, rather than on any single factor of the environment.

Light Intensity. — Certain experimental evidence indicates the importance of light intensity to nocturnal mice. Moody (1929) showed that P. m. gracilis can distinguish from darkness a light intensity of 1.13×10^{-6} candle power per square cm. It has been shown experimentally that the activity of deermice is related to the intensity of light. In very dim light or darkness they move about freely. As the light intensity increases, the activity of the deermice decreases until a threshold is reached at which they do not leave their nest boxes (Blair, 1943).

Kalabukhov (1938) studied the selection of several intensities of light by closely related species of Apodemus and Citellus and considered the results in relation to habitat restriction. He found that in a gradient apparatus Apodemus sylvaticus avoided bright illumination to a considerably greater degree than did A. flavicollis. In nature the former species seems to be the more strictly nocturnal of the two. Kalabukhov believed that A. sylvaticus lives in brushy and open habitats more commonly than A. flavicollis because the more strictly nocturnal habits of the former give it a greater degree of protection from predators. He found no marked difference between the reactions of 2 species of Citellus to light intensity.

The experiments discussed above indicate that light intensity has an influence of some importance on the activities of nocturnal mice. It is possible that light intensity has also some influence on habitat selection by mice, but this factor was not measured in the present investigation.

Food and Water. — The fact that the food and water required by Peromyscus m. bairdi and P. l. noveboracensis probably do not constitute an important factor in limiting their habitat distribution (Dice, 1922) has already been discussed. This conclusion, as to food, has been further substantiated by Cogshall (1928), who in the laboratory offered a choice of many different foods to the forms of Peromyscus mentioned above and also to P. m. gracilis and to P. m. sonoriensis.

Nesting Sites. — The possibility that Peromyscus l. noveboracensis is limited to woodlands and that P. m. bairdi is limited to open habitats because of a nesting site preference has been considered by Johnson (1926). He concluded from a few observations that nesting sites do not explain the habitat restrictions of these 2 species. On the other hand, Nicholson (1941) believed that P. l. noveboracensis showed a definite preference for artificial nest boxes placed above the ground. I have seen individuals of P. m. gracilis, when released from live traps, run into hollow logs, holes at the bases of stumps and trees, holes in tree trunks several feet above the ground, and occasionally into holes in the ground. My few observations suggest that gracilis usually uses refuges associated with tree trunks and stumps.

It is possible that the preference of a given race of Peromyscus for a particular type of nesting site may contribute to its restriction to a particular type of habitat. Much more critical study is required to ascertain the role of nesting site in habitat restriction of Peromyscus. In the experiments here described nesting site could not have been a deciding factor.

Interspecific Dominance. — There is no evidence that antagonism between P. m. bairdi and P. l. noveboracensis is an important factor in preventing one species from invading the habitat of the other (Dice, 1922). Observations have shown that these 2 species may in nature form mixed aggregations (Nicholson, 1941; Howard, 1949). Close association apparently may occur between 2 individuals of different species, for almost half of the double captures made with single-catch live traps included mice of 2 species (Evans and Holdenried, 1943). These writers remarked on the infrequency of fighting between 2 species of Peromyscus in the same live trap as compared with double captures of Peromyscus with Perognathus. In the Laboratory of Vertebrate Biology, groups of 3 individuals each of gracilis and bairdi commonly associated even when they had opportunity to live in separate cages (unpublished data of the author). These data accord with Dice's conclusion of a lack of interspecific antagonism and extend it to the 2 subspecies tested in the present study.

Other Factors. — Other factors also may influence the habitat preferences of Peromyscus, but none has been adequately treated in the literature from this viewpoint. For example, soil texture is important in the distribution of the kangaroo rat (Hardy, 1945:101). It is doubtful if soil type can be a factor which directly restricts bairdi to open habitats and gracilis to wooded or brushy ones. In its extension of range, bairdi has come to inhabit regions where soil was originally developed under woodland and has since been modified by agriculture and resulting soil erosion. Furthermore, bairdi usually excavates simple and shallow burrows and often uses abandoned burrows made by other species of animals (Howard, 1949). Also, my observations indicate that gracilis uses refuges associated with stumps, logs, or hollows in trees more frequently than it uses unprotected burrows in the soil.

Meteorological factors, food and water, nesting sites, intraspecific dominance, and soil type do not appear, separately, to be factors of importance in limiting the several kinds of Peromyscus to their particular habitats. Intensity of light is of importance in regulating the activity of nocturnal mice, but there is no good evidence that it is a factor which limits them to different habitats.

Limiting Factors Suggested by the Present Study

In the present study the reactions of 2 subspecies of Peromyscus maniculatus to contrasting types of simplified artificial habitats have been measured by experimental methods. The simplified habitat types were designed to simulate the characteristic vegetation of certain natural habitats: forest, grassland, and brushland.

It has been demonstrated that the artificial habitats in the experiments presented the main differences used by the mice in choosing between the 2 compartments of the reaction room. The artificial habitats were composed of objects made to resemble natural vegetation. Although the sections of tree trunks were less artificial than the grass made from Manila folders, they were not living. They were limited in height, and the environment surrounding them (with the exception of Experiment V) was devoid of cover, such as is provided by herbaceous plants in natural forest communities. Reduced to simple terms, habitat selection by gracilis and by bairdi seems to be based to at least a considerable extent on an attraction toward certain objects characteristic of their natural habitats. Thus, gracilis is attracted by tree trunks, while bairdi is attracted by grasslike objects.

The precise characteristics of the objects to which bairdi and gracilis responded were not ascertained in these experiments. P. m. bairdi may have responded to the shape of the grasslike objects, or possibly it responded to the close spacing of the artificial-grass blades, which may have given it a sense of security. P. m. gracilis, in turn, may have responded to the shape of tree trunks or trees, or it may have responded to objects which permitted it to climb upon them (Horner, 1948). Rigidity, as opposed to the flexibility of grass blades, might be an important characteristic of objects selected because of the arboreal adaptation of gracilis. The hypothesis, however, that habitat selection by gracilis is based on its arboreal adaptation is not supported by the experiments using jungle as one of the artificial habitats. The jungle supplied rigid objects suitable for use in climbing which were not similar to tree trunks. Yet gracilis showed no preference for jungle when it was given a choice between jungle and artificial grass (Experiment VI). On the other hand, no preference was shown for either jungle or tree trunks when they were presented for selection (Experiments VII and IX), and this result would be expected if habitat selection were based on a semiarboreal adaptation. Hence, the experiments involving jungle as one of the artificial habitats present conflicting evidence for the importance of semiarboreal adaptation in habitat selection by gracilis.

It is difficult to believe that the vegetation itself could ever be a direct cause of the death of an individual mammal that is not in its normal habitat. Evidence that a species of mammal may exist and apparently thrive in a habitat that it would not select if given a choice has been presented by Dice (1925). Normally the meadow vole, Microtus p. pennsylvanicus, lives in grassy areas. On Marion Island, Grand Traverse County, Michigan, however, this species was discovered living in fairly dense hardwood forest. It occurred there with other species of small mammals which are normally found in that type of habitat. Since most of the island was covered with forest and only small areas of open land were present, Microtus here had little choice of habitat.

It appears likely, therefore, that objects in the environments of the several forms of Peromyscus present cues by which these mice select their preferred habitats, but that under certain circumstances some animals can exist in habitats which they would not normally select.

Evidence that animals use cues in their selection of habitats has been presented by Lack (1933). He studied the birds that occurred in pine plantations of different ages and heights in England. By comparing the habitats in which particular species lived, he concluded that the cue for habitat selection by certain species of birds was apparently the height of the vegetation rather than its type. Other species seemed to react to preferred types of singing perches or nesting sites. Such factors Lack referred to as psychological factors.

The results of my experiments suggest that in nature objects, such as the type of plant, may be the cues by which the various races of Peromyscus select their habitats. To what extent this may be true of other kinds of animals is unknown.

It seems likely that a species is adapted to the objects which it uses as cues in selecting its habitat. For instance, the long-tailed forest-inhabiting forms of Peromyscus have been shown by Horner (1948) to possess a definite semiarboreal adaptation in comparison with the short-tailed forms which inhabit open fields. One of these long-tailed forms, P. m. gracilis, has been shown in this paper to select tree trunks in preference to artificial grass, which are objects to which it is adapted in its natural environment. Peromyscus leucopus noveboracensis, another long-tailed woodland form, likewise has shown in its use of artificial nest boxes a preference for nesting sites situated above the ground (Nicholson, 1941).

HEREDITY OF HABITAT SELECTION

Most animals tested in the first 3 experiments were field caught. Because it was not known at the beginning of the study whether habitat selection is due to conditioning or to instinct, it was thought that individuals previously conditioned in nature would react more strongly to the artificial habitats than laboratory-bred mice. A constant supply of field-caught Peromyscus m. gracilis was impossible to obtain, however, and only laboratory-bred mice of both subspecies were tested in Experiment IV and in subsequent experiments.

Because the laboratory-bred animals were kept in standard laboratory cages, they had had no previous experience either with natural or with artificial habitats of the type used in these experiments. In view of their lack of previous experience, it is concluded that the habitat preferences expressed in these experiments must have resulted from instinctive behavior.

Further information on the heredity of artificial-habitat selection was obtained in Experiment X by testing F_1 hybrids produced by matings between individuals of female bairdi and male gracilis. The 7 hybrid individuals tested exhibited a preference for the artificial-grass habitat which was contrasted with the tree trunks. This preference was significant at the 5 per cent level for one measurement and at the 1 per cent level for 3 measurements of habitat selection (Table XIX). Thus, the genetic mechanism responsible for selection of artificial grass is at least partly dominant over that responsible for the selection of tree trunks. The

TABLE XIX

Summary of Selection Between Artificial-grass and Tree-trunk Habitats by Peromyscus m. bairdi x P. m. gracilis F_1 Hybrids in Experiment X.

Light Intensity (in f.c.)	Habitat with the Higher Mean			
	Total Time in Habitat	Activity-Wheel Turns	Seeds Eaten	Water Consumed
Dark	grass††	grass†	grass††	grass††

† Represents a value significant at the 5 per cent level.
†† Represents a value significant at the 1 per cent level.

F values for the several measurements of habitat selection by the hybrids were, in general, lower than those for the parental subspecies. Also, there was a significant variation among the hybrid individuals for the measures of wheel turns, seeds eaten, and water consumed. This indicates a greater degree of variability in habitat selection by the hybrids than by either of the parents, bairdi or gracilis.

It is probably true that the first instinctive act of an animal may be reinforced by learning and conditioning, but this in no way invalidates the conclusion that artificial-habitat selection is based on instinctive behavior. There is no evidence in the experiments to show that instinctive acts of an animal may be reinforced in this manner. Such a reinforcement would have to appear during the 4-day test given each mouse. Each mouse varied from day to day in the proportion of its reactions in each artificial habitat, and each mouse differed in this respect from every other mouse. There was no consistent trend among the mice toward a more definite habitat selection as the 4-day test periods progressed.

Habitat selection in nature, however, is probably not entirely an instinctive process. These experiments deal only with artificial habitats that differ widely from each other, such as forest contrasted with open fields. Selection of more local conditions within such habitats might well be modified by experience as suggested by Miller (1942:34).

The instinctive selection of objects in the habitat may be assumed, in accordance with the modern theory of evolutionary processes, to have developed in animals in response to natural selection. The evolutionary importance and significance of habitat selection have been discussed by Elton (1930), Lack (1933, 1940), Miller (1942), and Thorpe (1945).

SUMMARY

In nature mice of the subspecies Peromyscus maniculatus bairdi are closely restricted to open-field habitats, while the subspecies P. m. gracilis lives most commonly in hardwood forests and to a lesser extent in brushy habitats. To ascertain the factors responsible for these habitat preferences, selection for artificial habitats by bairdi and gracilis was measured under controlled experimental conditions.

The artificial habitats presented to the 2 races of Peromyscus were tree trunks, artificial grass, and jungle, the last composed of a latticework of sticks. Selection by individual mice between 2 of these artificial habitats was made possible in each of 10 experiments by placing a different artificial habitat in each of 2 compartments of a reaction room. The habitat preference of each mouse was measured for 4 consecutive nights by recording (1) the number of sunflower seeds eaten, (2) the amount of water drunk, (3) the number of turns made in activity wheels, and (4) the total time spent in each of the 2 artificial habitats. The data obtained from these measurements were treated statistically.

In these experiments, bairdi is shown to have selected the artificial-grass habitat in preference to either the tree-trunk or the jungle habitat. The differences in this preference were significant at the 5 per cent or at the 1 per cent level for 9 out of 12 measurements involving 3 experiments. The tree-trunk habitat was selected by gracilis in those experiments in which this habitat was contrasted with the artificial-grass habitat. The differences in preference between these 2 artificial habitats were also significant at the 5 per cent or at the 1 per cent level for 9 out of 12 measurements involving 3 experiments.

The selection of these 2 artificial habitats by the 2 races of Peromyscus seems to be a selection for particular kinds of objects in the environment. These objects probably act as cues by which the mice recognize the environment most suitable to them.

Selection of the artificial-grass habitat by bairdi and of the tree-trunk habitat by gracilis was successfully made in darkness both by normal mice and by mice from which the vibrissae had been removed. These results indicate that for its habitat selection Peromyscus is independent both of sight and of the tactile sense mediated through the vibrissae.

Laboratory-bred Peromyscus which had had no previous experience either with natural habitats or with artificial habitats simulating natural ones were tested in some of the experiments.

Each subspecies exhibited a preference for the type of habitat which it normally inhabited in nature. It may be concluded, therefore, that habitat selection by Peromyscus is basically genetic in nature. The trait of selection for the artificial-grass habitat is, to some extent, dominant in heredity over the trait of selection for the tree-trunk habitat. This is demonstrated by the preference of F_1 bairdi x gracilis hybrids for the artificial-grass habitat over the tree-trunk habitat. The preference was statistically significant in all 4 measurements of habitat selection.

LITERATURE CITED

BLAIR, W. FRANK

1940 A study of prairie deer-mouse populations in southern Michigan. Amer. Midl. Nat., 24: 273-305.

1942 Size of home range and notes on the life history of the woodland deer-mouse and eastern chipmunk in northern Michigan. Journ. Mammalogy, 23: 27-36.

1943 Activities of the Chihuahua deer-mouse in relation to light intensity. Journ. Wildlife Management, 7: 92-97.

CHENOWETH, HOMER E.

1917 The reactions of certain moist forest mammals to air conditions and its bearing on problems of mammalian distribution. Biol. Bull., 32: 183-201.

COCHRAN, WILLIAM G., and GERTRUDE M. COX

1950 Experimental designs. New York: John Wiley and Sons. Pp. ix+454.

COGSHALL, ANNETTA STOW

1928 Food habits of deer mice of the genus Peromyscus in captivity. Journ. Mammalogy, 9: 217-21.

DICE, LEE R.

1922 Some factors affecting the distribution of the prairie vole, forest deer mouse, and prairie deer mouse. Ecology, 3: 29-47.

1925 The mammals of Marion Island, Grand Traverse County, Michigan. Occ. Papers Mus. Zool. Univ. Mich., 160: 1-8.

1929 A new laboratory cage for small mammals, with notes on methods of rearing Peromyscus. Journ. Mammalogy, 10: 116-24.

1931a The occurrence of two subspecies of the same species in the same area. Ibid., 12: 210-13.

1931b The relation of mammalian distribution to vegetation types. Sci. Mo., 33: 312-17.

1933 Fertility relationships between some of the species and subspecies of mice in the genus Peromyscus. Journ. Mammalogy, 14: 298-305.

1945 Minimum intensities of illumination under which owls can find dead prey by sight. Amer. Nat., 79: 385-416.

1947 Effectiveness of selection by owls of deer-mice (Peromyscus maniculatus) which contrast in color with their background. Contrib. Lab. Vert. Biol. Univ. Mich., 34: 1-20.

DICE, LEE R., and SHERMAN A. HOSLETT

1950 Variation in the spontaneous activity of Peromyscus, as shown by recording wheels. Contrib. Lab. Vert. Biol. Univ. Mich., 47: 1-18.

DICE, LEE R., and H. B. SHERMAN

1922 Notes on the mammals of Gogebic and Ontonagon counties, Michigan, 1920. Occ. Papers Mus. Zool. Univ. Mich., 109: 1-47.

ELTON, CHARLES

1927 Animal ecology. London: Sidgwick and Jackson. Pp. xxi + 207.

1930 Animal ecology and evolution. Oxford: Clarendon Press. Pp. 96.

EVANS, F. C., and R. HOLDENRIED

1943 Double captures of small rodents in California. Journ. Mammalogy, 24: 401.

GOULDEN, C. H.

1939 Methods of statistical analysis. New York: John Wiley and Sons. Pp. vii + 277.

GRINNELL, JOSEPH

1917 Field tests of theories concerning distributional control. Amer. Nat., 51: 115-28.

HARDY, ROSS

1945 The influence of types of soil upon the local distribution of some mammals in southwestern Utah. Ecol. Monog., 15: 71-108.

HARRIS, VAN T.

1950 An experimental study of habitat selection by the deermouse, Peromyscus maniculatus. Publ. No. 1693. Ann Arbor: Univ. Microfilms. 170 pp. (Ph.D. thesis.)

HOOPER, EMMET T.

1942 An effect on the Peromyscus maniculatus rassenkreis of land utilization in Michigan. Journ. Mammalogy, 23: 193-96.

HORNER, ELIZABETH B.

1948 Arboreal adaptation of Peromyscus, with special reference to the use of the tail. Publ. No. 951. Ann Arbor: Univ. Microfilms. 182 pp. (Ph.D. thesis.)

HOWARD, WALTER E.

1949 Dispersal, amount of inbreeding, and longevity in a local population of prairie deermice on the George Reserve, southern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 43: 1-50.

JOHNSON, M. S.

1926 Activity and distribution of certain wild mice in relation to biotic communities. Journ. Mammalogy, 7: 245-77.

KALABUKHOV, N. I.

1938 On ecological character of closely related species of rodents. 1. The peculiarities of the reaction of wood-mice (Apodemus sylvaticus L. and A. flavicollis Melch.) and ground-squirrels (Citellus pygmaeus Pall. and C. suslicus Gueld.) to the intensity of illumination. Zool. Zhurn., 17: 521-32. (In Russian, with English summary.)

LACK, DAVID

1933 Habitat selection in birds with special reference to the effects of afforestation on the Breckland avifauna. Journ. Animal Ecol., 2: 239-62.

1940 Habitat selection and speciation in birds. Brit. Birds, 34: 80-84.

MILLER, A. H.

1942 Habitat selection among higher vertebrates and its relation to intraspecific variation. Amer. Nat., 76: 25-35.

MOODY, P. A.

1929 Brightness vision in the deer-mouse, Peromyscus maniculatus gracilis. Journ. Exper. Zool., 52: 367-405.

NICHOLSON, ARNOLD J.

1941 The homes and social habits of the wood-mouse (Peromyscus leucopus noveboracensis) in southern Michigan. Amer. Midl. Nat., 25: 196-223.

OSGOOD, WILFRED H.

1909 Revision of the mice of the American genus Peromyscus. U. S. Dept. Agric., N. Amer. Fauna, 28: 1-285.

RICHTER, C. P., and G. H. WANG

1926 New apparatus for measuring the spontaneous motility of animals. Journ. Lab. and Clin. Med. 12: 289-92.

SHELFORD, V. E.

1911 Physiological animal geography. Journ. Morphol., 22: 551-618.

SMITH, JAMES G., and ACHESON J. DUNCAN

1945 Sampling statistics and applications. 1st. ed.; New York: McGraw-Hill Book Co. Pp. xii + 498.

Smithsonian Institution

1918 Smithsonian meteorological tables. 4th rev. ed. Smithsonian Misc. Coll., 69 (1): i-lxxii, 1-261.

SUMNER, F. B.

1932 Genetic, distributional, and evolutionary studies of the subspecies of deer mice (Peromyscus). Biblio. Genetica 9: 1-106.

THORPE, W. H.

1945 The evolutionary significance of habitat selection. Journ. Animal Ecol., 14: 67-70.

WOOD, FRANK E.

1910 A study of the mammals of Champaign County, Illinois. Bull. Ill. State Lab. Nat. Hist., 8: 501-613.

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price, $0.75.

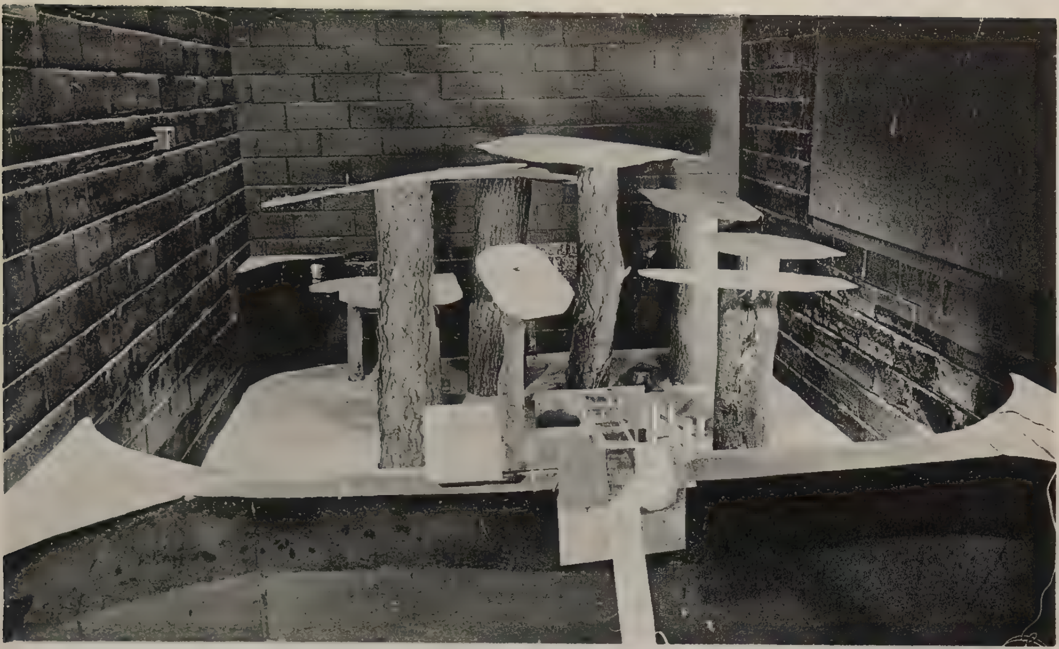


FIG. 1. The artificial tree-trunk habitat in a compartment of the reaction room. In the foreground is the partition which separates the tree-trunk compartment from the artificial-grass compartment. The runway across this partition, together with part of the recording apparatus, is in the middle foreground.

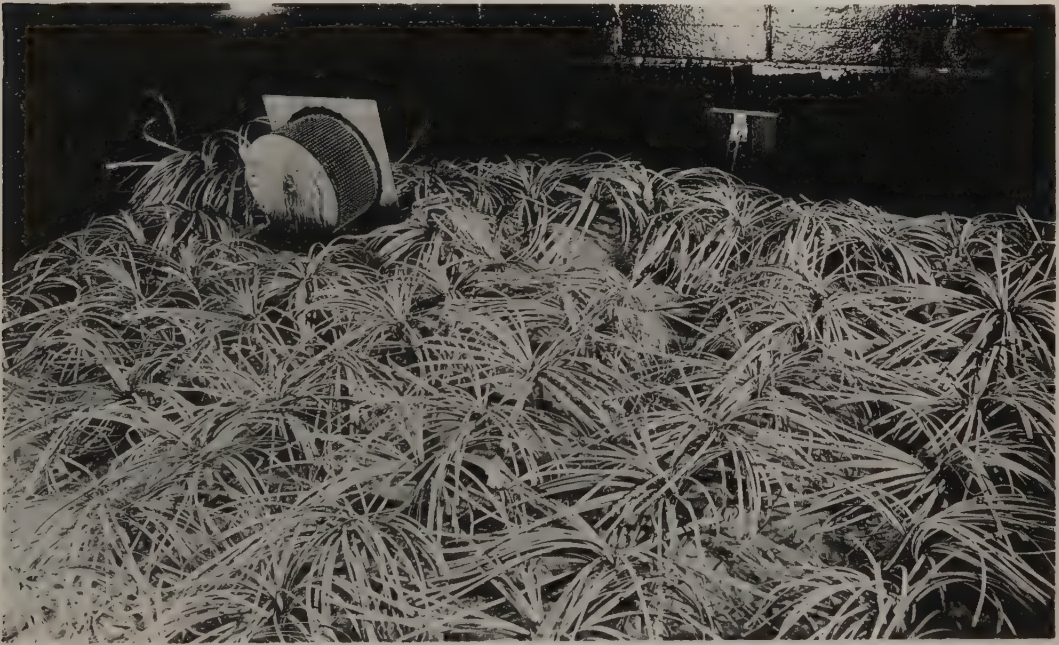


FIG. 2. Part of the artificial-grass habitat in a compartment of the reaction room. The activity wheel is in the left background and the water tube and rack in the center background.

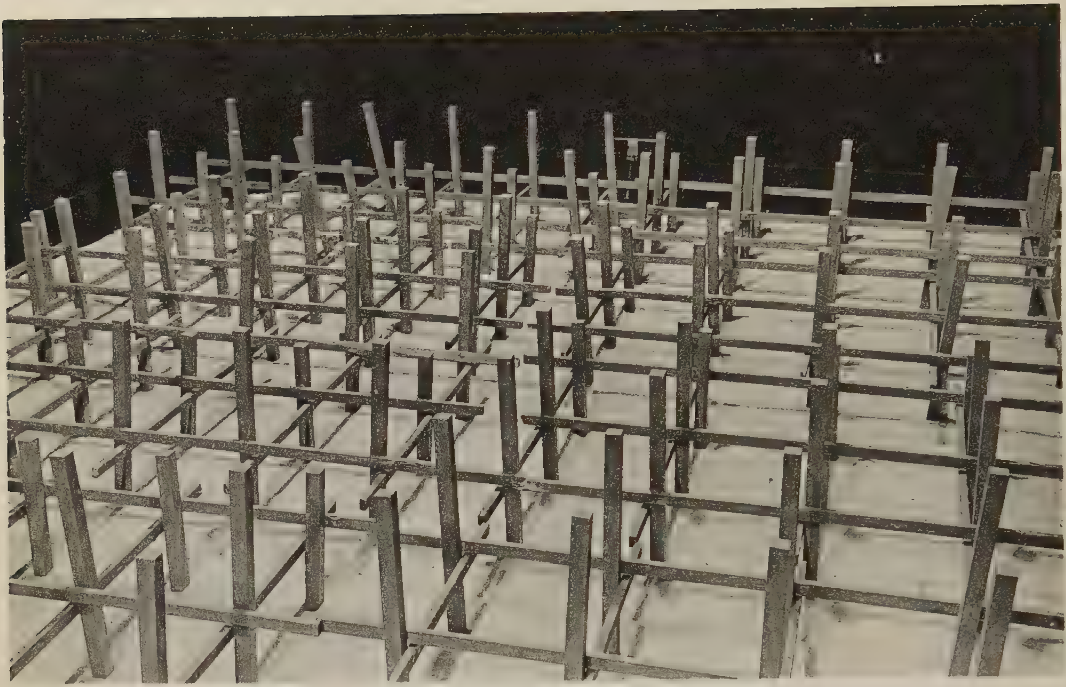


FIG. 1. The artificial jungle habitat.

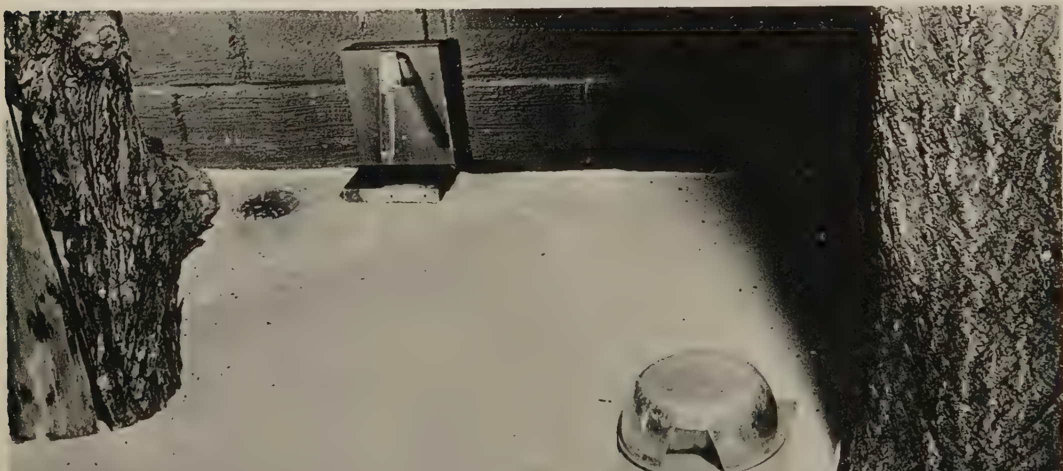


FIG. 2. An experimental compartment. Left to right: tree trunk, food dish, water tube and rack, nest box, and tree trunk.

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

University of Michigan, Ann Arbor, Michigan

Number 57 June, 1952

VARIATION IN BODY DIMENSIONS AND PELAGE COLOR OF CERTAIN LABORATORY-BRED STOCKS OF THE PEROMYSCUS TRUEI GROUP

By LEE R. DICE

Accepted for publication Nov. 27, 1951

CONTENTS

Introduction 1
Methods of Study 2
Collecting Stations 3
Variation Due to Age. 6
Variation Related to Sex 7
Variation in Dimensions and Weight. 9
Variation in Pelage Color 15
Pelage Color of Hybrids 20
Fertility Relations 20
Systematics 22
Summary 24
Literature Cited 24

INTRODUCTION

THE variation in dimensions of the body and skeleton and in the pelage color of certain laboratory-bred stocks belonging to 3 species of the Peromyscus truei group of small rodents is described in this report. The parents of these stocks were originally captured in the states of Arizona, Colorado, New Mexico, and Texas.

The Peromyscus truei group consists, according to Hoffmeister (1951), of 4 species: truei, nasutus, bullatus, and difficilis. To these must be added the species comanche of Blair (1943).

Hoffmeister considers comanche to be a subspecies of nasutus, a conclusion which I cannot accept because of partial infertility between these forms. The species group ranges from Oregon to Colorado and southward to Texas and over the highlands of Mexico, including Baja California. They are mice of fairly large size. All of them have conspicuous ears, which in truei are exceptionally large. In the United States these mice generally occupy xeric habitats of open woodland and brush on the mountain slopes, but certain populations live in rock and shrub-covered habitats on the xeric parts of the high plains. Peromyscus truei sometimes ascends into the open coniferous-forest habitats of the lower part of the montane belt. In many areas the 2 species truei and nasutus occur together, sometimes in the same habitats, but without interbreeding (Dice, 1942).

Acknowledgments

The expense of rearing the Peromyscus which are here described was in part borne by the Museum of Zoology, in part by the Laboratory of Vertebrate Biology, and in part by research grants from the Faculty Research Fund, University of Michigan. The several expeditions on which most of the breeding stocks were secured were supported in part by the Museum of Zoology, Laboratory of Vertebrate Biology, Carnegie Institute of Washington, and Cranbrook Institute of Science, by special gifts from Bryant Walker and from W. P. Harris, Jr., and by contributions from the members of the expeditions. The Tule Canyon stock was presented by Milton F. Landwer. The B, C, and E stocks from Highrolls were presented by Philip M. Blossom.

For the tabulation of the measurements and for the statistical computations I am indebted to John A. King and to William Prychodko. The map and figures were drawn by Grace Yesley.

METHODS OF STUDY

All the mice herein described were born in the laboratory and after being reared under standard conditions to an approximate age either of 1 year or of 2 years were killed and prepared as specimens. The body measurements were made by myself immediately after each animal had been killed by ether and while it was still completely relaxed (Dice, 1932: 5-7). The measurements of the cleaned skull and femur and the color readings were made by various assistants.

For the measure of pelage color 2 methods have been employed. Reflection-meter readings of the flat skins were made with a Photovolt reflection meter according to the method previously described by me (Dice, 1947: 5). For several of the stocks tint-photometer readings were made in the same manner and by the same Hess-Ives instrument as those previously made by myself of other specimens of Peromyscus (Dice, 1932: 19). The readings by both instruments are given in terms of the percentage of light of the specified color which is reflected from the specimen in comparison with the amount reflected from a magnesium carbonate block, the reflectance of which is taken to be 100 per cent. The color screens used in the 2 instruments differ in the wave lengths of light they transmit and consequently their readings are not fully comparable.

For the calculation of variances and standard deviations, the sum of the squared deviations from the mean has been divided by n - 1. The significance of differences between means has been mostly estimated by the method of Dice and Leraas (1936), in which the t value of significance is taken to be about 2.7. For more critical comparisons the t value of the difference between each pair of means has been calculated separately.

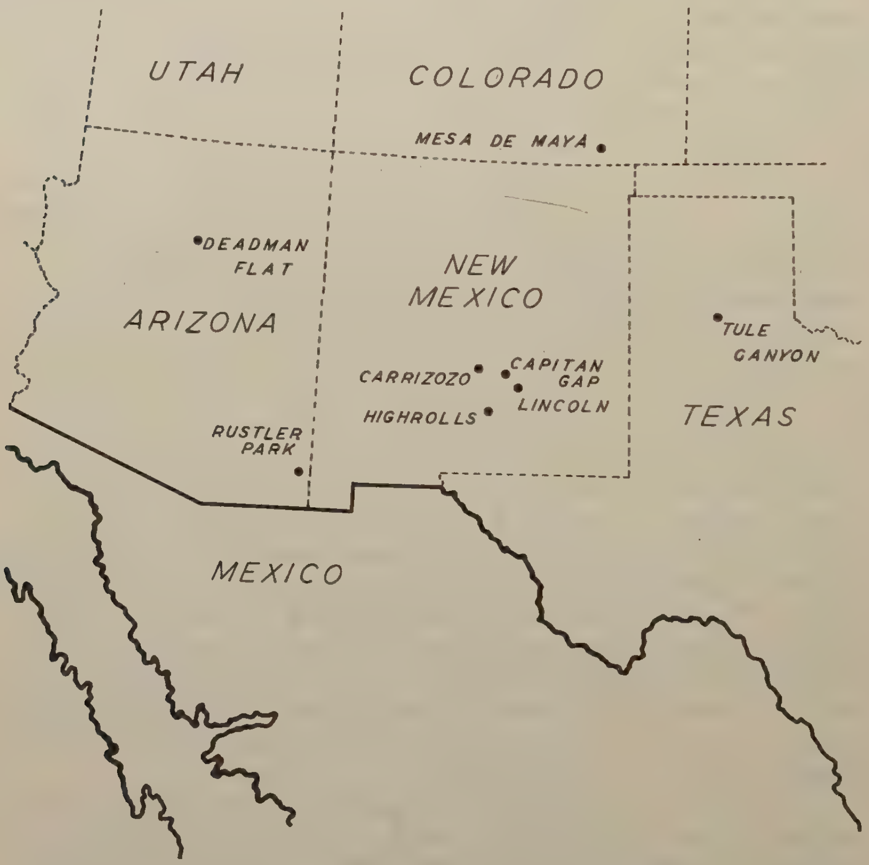
COLLECTING STATIONS

The parents of the breeding stocks used in these studies were originally collected at the following stations:

Capitan Gap. — Peromyscus truei truei. Near Capitan Gap, Capitan Mountains, Lincoln County, New Mexico, 6 miles northeast of Capitan, in mixed pinyon-juniper and yellow pine habitat. Taken by Lee R. Dice in 1937 on an expedition supported jointly by the Laboratory of Vertebrate Biology, Museum of Zoology, and the Carnegie Institution of Washington. Four field-caught females and 6 males were the parents of the laboratory-bred stock, of which only 7 individuals were in any way inbred.

Carrizozo. — Peromyscus nasutus griseus Benson. From the black lava of the Tularosa Malpais, 4 miles northwest of Carrizozo, Lincoln County, New Mexico. Various individuals were trapped by G. W. Bradt in 1928 and 1929 (Bradt, 1932), by S. B. Benson in 1931, and by Lee R. Dice in 1937, on expeditions supported in part by the Carnegie Institution of Washington, in part by the Museum of Zoology, and in part by the Laboratory of Vertebrate Biology. The considerably inbred laboratory stock was derived from 2 field-caught females and 2 males.

Deadman Flat. — Peromyscus truei truei. From rabbitbrush habitat in Deadman Flat, 15 to 20 miles north of Flagstaff, Coconino County, Arizona. Taken in 1932 by members of an expedition, led by G. W. Bradt and including R. K. Knox, A. J. Nicholson, A. M. Stebler, and H. J. Walt, which was supported in part by the Carnegie Institution of Washington. The laboratory-bred stock was derived from 4 field-caught females and 3 males. Of the 1 year age class only 1 individual was inbred, but of the 2-year class about half were more or less inbred.



MAP 1. Localities at which the stocks were collected.

Highrolls A. — Peromyscus truei truei. From pinyon-juniper woodland 1/2 mile west of Highrolls, Otero County, New Mexico (Dice, 1930). Taken in the summer of 1927 by G. W. Bradt, Robert Bradley, S. C. Whitlock, and Lee R. Dice, on an expedition from the Museum of Zoology supported in part by Bryant Walker and by W. P. Harris, Jr. The laboratory stock consists of a single sibship derived from a pair of field-caught animals.

Highrolls B, C, and E. — Peromyscus nasutus nasutus. From vicinity of Highrolls, Otero County, New Mexico. Taken in summer of 1936 by Philip M. Blossom. Station B is located 1-1/2 miles west of Highrolls at 6000 feet, in mountain mahogany and sumac habitat, just below the pinyon-juniper belt. Station C is 1 mile west of Highrolls at 6300 feet, near the lower limit of the pinyon-juniper belt. Station E is 3 miles east of Highrolls at an elevation of 7500 feet near the upper limit of the pinyon-juniper belt. These stocks were used only for testing intraspecific fertility and are not included in the tables of measurements.

Lincoln. — Peromyscus nasutus nasutus. From mountain slopes covered with pinyon-juniper woodland 4 miles northwest of Lincoln, in Lincoln County, New Mexico, near a locality called "Double-crossing." Taken in 1937 by Lee R. Dice on an expedition supported jointly by the Laboratory of Vertebrate Biology, Museum of Zoology, and the Carnegie Institution of Washington. The laboratory stock was derived without inbreeding from 6 field-caught females and 3 males.

Mesa de Maya. — Peromyscus truei truei. From pinyon and juniper habitat at the north base of the Mesa de Maya, in Las Animas County, Colorado, about 45 miles east of Trinidad. Taken by Lee R. Dice in 1925 on an expedition from the Museum of Zoology which was supported in part by the Carnegie Institution of Washington. A single pregnant female taken in the field in 1925 gave birth in the laboratory to 2 sons, one of which died and the other was mated to his mother to produce this highly inbred stock.

Rustler Park. — Peromyscus nasutus nasutus. From yellow-pine habitat in Rustler Park, upper part of the Chiricahua Mountains, Cochise County, Arizona. Taken in summer of 1932 by Victor Cahalane on an expedition from Cranbrook Institute of Science which was in part sponsored by the Desert Laboratory of the Carnegie Institution of Washington. The laboratory stock was derived from 3 field-caught females and 3 males. About one-third of the individuals both in the 1-year and 2-year age classes were somewhat inbred.

Tule Canyon. — Peromyscus comanche Blair (1943). From the rocky slopes of Tule Canyon, 22 miles east of Tulia, in Briscoe County, Texas. Trapped in 1932 by Milton F. Landwer. The laboratory stock was produced from 3 field-caught females and 3 males. Three of the individuals in the 1-year age class and 6 in the 2-year class were somewhat inbred.

VARIATION DUE TO AGE

For the measure of age variation in the body and skeletal dimensions of the mice there are available, for 5 stocks, series of specimens both of the 1-year (36-78 weeks) and of the 2-year (79 and up weeks) age classes (Table I).

TABLE I

Differences in Dimensions and in Pelage Color between 2-year and 1-year Age Classes in the Peromyscus truei Group

Mean of the 2-year class minus mean of the 1-year class and standard error of the differences. Males and females are combined in each age class. Measurements of body dimensions in millimeters, of pelage color in reflection-meter readings.

Character	truei		nasutus	griseus	comanche
	Deadman Flat	Mesa de Maya	Rustler Park	Carrizozo	Tule Canyon
Dimensions					
Body length	1.52 ± .94	4.68 ± .78	4.27 ± .80	3.97 ± .70	2.58 ± .74
Tail length	.06 ± 1.11	4.36 ± .83	1.76 ± 1.23	2.55 ± 1.60	1.94 ± 1.22
Hind foot length	-.326 ± .167	.230 ± .111	.296 ± .156	.345 ± .122	.080 ± .182
Ear length	.409 ± .248	1.233 ± .178	.328 ± .214	.783 ± .176	.249 ± .249
Femur length	-.009 ± .146	.868 ± .107	.709 ± .126	.385 ± .173	.429 ± .143
Mandible length	.254 ± .106	.716 ± .100	.550 ± .124	.496 ± .109	.450 ± .117
Condyle-premaxilla length	.218 ± .147	.784 ± .100	.754 ± .141	1.031 ± .170	.432 ± .153
Condyle-zygoma length	.203 ± .101	.433 ± .069	.389 ± .094	.379 ± .132	.297 ± .108
Bullar Width	.013 ± .069	.166 ± .042	.177 ± .062	.292 ± .052	.154 ± .072
Reflection-meter readings					
Dorsal stripe					
Red	1.26 ± .51	.98 ± .51	.18 ± .31	-1.06 ± .45	.34 ± .44
Green	-.02 ± .27	.65 ± .34	.15 ± .21	.49 ± .25	.50 ± .24
Blue	-.19 ± .18	.15 ± .24	-.17 ± .14	-.18 ± .15	.46 ± .19
Side stripe					
Red	1.67 ± .72	.86 ± 1.00	.62 ± .54	.19 ± .71	1.81 ± .99
Green	.17 ± .45	.93 ± .48	.17 ± .37	.44 ± .47	1.32 ± .52
Blue	-.31 ± .29	.18 ± .31	.12 ± .22	.13 ± .31	.35 ± .33

In hind-foot length the Mesa de Maya 2-year-old mice exceed the 1-year mice by an average of .230 ± .111 mm, an amount which is significant at the 5 per cent level. The Deadman Flat 2-year class averages smaller in this measurement than the 1-year class by .326 ± .167mm, an amount which is close to the 5 per cent level of significance. In the other 3 stocks here compared, the 2 age classes do not differ significantly from one another in foot length. I conclude that in the truei group there is no good evidence for growth in foot length between the first and second years of life.

In all the other measurements of the body and skeleton the 2-year–old mice exceed the 1-year class, the only exception being for femur length in the Deadman Flat stock, in which the 1-year class averages .009 ±.146 mm the larger, a nonsignificant difference. For the several measurements the excess of the 2-year over the 1-year animals ranges in the various stocks from not significant to highly significant. For no measurement is the difference between the age classes significant at the 1 per cent level for all the stocks. For mandibular length and condylo-zygomatic distance the 2-year mice significantly exceed the 1-year mice at the 5 per cent level in all the stocks. For the other measurements the age classes fail to differ significantly in all the stocks, though they always do so in at least 1 stock. The general impression is that except for length of hind foot, the 2-year old mice average slightly larger in nearly all of their measurements than the 1-year mice.

The differences in pelage color readings between the 2-year and 1-year old mice are not very great and are inconsistent among the 5 stocks here compared. For no color reading are the differences between the age classes significant in all 5 stocks. Most of the differences are statistically insignificant. So far as these measurements can be relied upon, there is no evident difference in pelage color between the 1-year and 2-year age classes in the truei group.

VARIATION RELATED TO SEX

For the analysis of the effects of sex on variation in these mice, the measurements of body dimensions and of pelage color of the males and females of the 1-year age class of 2 stocks are compared in Table II. It is evident from this table that in most of their dimensions the males and females do not differ significantly. In ear length the males average larger than the females and in the Deadman Flat stock the difference is significant at the 5 per cent level, but in the Capitan Gap stock the difference between the sexes in this measurement is not significant. The females of the Capitan Gap stock average longer in mandibular length than the males, the difference being significant at the 5 per cent level. The males of the Deadman Flat stock, however, exceed the females in this measurement, though the difference is not significant. I conclude that there is no consistent difference between the sexes in these stocks of mice in any dimension of the body or skeleton.

TABLE II

Differences in Dimensions and in Pelage Color between Males and Females of Peromyscus truei

Means of the measurements of the males minus means of the females and the standard errors of the differences. Measurements of body dimensions in millimeters, of pelage color in reflection-meter readings; 1-year age class.

Character	Capitan Gap	Deadman Flat
Dimensions		
Body length	-.90 ± .80	1.36 ± 1.16
Tail length	-2.36 ± 1.44	-.60 ± 1.29
Foot length	.108 ± .116	.210 ± .214
Ear length	.096 ± .183	.620 ± .281
Femur length	-.253 ± .172	.034 ± .161
Mandible length	-.186 ± .079	.147 ± .124
Condyle-premaxilla length	-.103 ± .127	.056 ± .131
Condyle-zygoma length	-.128 ± .090	.074 ± .093
Bullar width	-.025 ± .062	-.015 ± .049
Reflection-meter readings		
Dorsal stripe		
Red	.40 ± .36	-.76 ± .63
Green	.03 ± .17	-.36 ± .33
Blue	.09 ± .15	-.04 ± .24
Side stripe		
Red	-.31 ± .71	-2.60 ± 1.17
Green	1.42 ± .42	.44 ± .54
Blue	.80 ± .27	.28 ± .33

The reflection-meter readings of pelage color also fail to exhibit any consistent difference between the sexes. In the Capitan Gap stock the males of the 1-year class significantly exceed the females in readings for green and for blue of the light reflected from the side of the body, but in the Deadman Flat stock the females exceed the males in the readings of red from the side stripe. In all the other color readings the sexes do not differ significantly.

In view of the lack of any consistent difference in the truei group between the males and females in any body or skeletal dimension or in pelage color, I have combined the measurements for the 2 sexes in the analysis of other aspects of variation among these mice.

The failure to discover consistent differences in dimensions or in pelage color between the males and females of the truei group is at variance with the conditions in some other species of Peromyscus. In Peromyscus maniculatus (Dice, 1932, 1933a) and in P. leucopus (Dice, 1937) the males average larger than the females in hind-foot length. In leucopus the males also may exceed the females in average body length. In the species polionotus, on the contrary, the females exceed the males in certain measurements (Sumner, 1926), though not in foot length (Hayne, 1950). In Peromyscus eremicus, also, the females average larger than the males and, in addition, they average slightly paler than the males in pelage color (Dice, 1939).

Sexual dimorphism in dimensions and in pelage color seems consequently to be a highly individual matter among the mice of the genus Peromyscus. In certain species the males average the larger in certain dimensions, while in other species the females average larger than the males in these same dimensions. Hayne (1950) has shown that, even within a single subspecies, a stock from one locality may exhibit sexual dimorphism in certain dimensions, while a neighboring stock may fail to show any significant difference between the sexes in these particular characters.

VARIATION IN DIMENSIONS AND WEIGHT

None of the stocks averages consistently larger or smaller than all the others in any dimension of the body or skeleton, though certain stocks do rank significantly larger or smaller than most of the others in one or more measurements.

In body length the Capitan Gap stock, which has a mean of 107.66 mm for the 1-year class, averages significantly longer than all the other stocks (Table III). The Lincoln, Rustler Park, Tule Canyon, and Deadman Flat stocks all average significantly longer than the Carrizozo stock, which in its turn significantly exceeds the Highrolls and Mesa de Maya stocks. The Mesa de Maya mean is 97.12 mm.

Tail length exhibits the greatest amount of variation among the stocks of any of the measurements here taken, ranging from a mean of 115.53 mm for the 1-year old mice of the Rustler Park stock to only 87.79 mm for the Mesa de Maya stock (Fig. I). The Rustler Park stock significantly exceeds in this measurement the Lincoln stock, which in its turn significantly exceeds all the others. The Mesa de Maya stock averages significantly shorter in tail length than all the other stocks. The Tule Canyon stock significantly

TABLE III

Measurements of the Peromyscus truei Group

Means, standard errors, and standard deviations in millimeters.

Stock	Age Class	Sex	No.	Field-caught Parents	Mean Age (in Weeks)	Body Length	Tail Length	Hind-foot Length	Ear Length
truei									
Capitan Gap	1 yr.	♂♂	41	10	56	107.24 ± .52 (3.34)	93.13 ± 1.01 (6.20)	23.028 ± .058 (.370)	25.242 ± .123 (.758)
	1 yr.	♀♀	36	7	53	108.14 ± .60 (3.62)	95.49 ± 1.03 (6.10)	22.920 ± .100 (.590)	25.146 ± .135 (.748)
	1 yr.	♂♀	77	10	55	107.66 ± .40 (3.48)	94.26 ± .73 (6.23)	22.977 ± .069 (.598)	25.196 ± .091 (.773)
Deadman Flat	1 yr.	♂♂	27	7	62	104.52 ± .86 (4.48)	91.27 ± .90 (4.21)	23.719 ± .153 (.796)	26.533 ± .195 (1.015)
	1 yr.	♀♀	32	6	54	103.16 ± .78 (4.40)	91.87 ± .93 (5.09)	23.509 ± .149 (.843)	25.913 ± .202 (1.145)
	1 yr.	♂♀	59	7	58	103.78 ± .58 (4.45)	91.62 ± .65 (4.70)	23.605 ± .107 (.821)	26.197 ± .146 (1.123)
	2 yr.	♂♀	33	5	103	105.30 ± .74 (4.27)	91.68 ± .90 (4.49)	23.279 ± .128 (.737)	26.606 ± .200 (1.148)
Highrolls A	1 yr.	♂♀	20	2	61	97.40 ± 1.02 (4.56)	95.22 ± 2.04 (6.12)	22.885 ± .107 (.479)	25.080 ± .171 (.764)
Mesa de Maya	1 yr.	♂♀	52	2	47	97.12 ± .44 (3.16)	87.79 ± .51 (3.52)	22.808 ± .081 (.587)	23.272 ± .119 (.841)
	2 yr.	♂♀	40	2	124	101.80 ± .64 (4.08)	92.15 ± .65 (3.74)	23.038 ± .076 (.481)	24.505 ± .132 (.811)
nasutus									
Lincoln . . .	1 yr.	♂♀	64	9	53	104.89 ± .37 (2.94)	103.73 ± .61 (4.84)	23.275 ± .064 (.510)	22.435 ± .096 (.765)
Rustler Park	1 yr.	♂♀	44	6	51	104.70 ± .58 (3.83)	115.53 ± .68 (4.79)	23.269 ± .109 (.764)	21.981 ± .109 (.712)
	2 yr.	♂♀	36	6	118	108.97 ± .55 (3.22)	117.29 ± 1.02 (5.67)	23.565 ± .111 (.649)	22.309 ± .184 (1.041)
griseus									
Carrizozo . .	1 yr.	♂♀	78	4	55	100.78 ± .33 (2.94)	92.40 ± .58 (4.80)	22.186 ± .037 (.330)	22.541 ± .087 (.750)
	2 yr.	♂♀	32	3	140	104.75 ± .62 (3.52)	94.95 ± 1.49 (6.97)	22.531 ± .116 (.659)	23.324 ± .153 (.767)
comanche									
Tule Canyon	1 yr.	♂♀	54	6	53	104.11 ± .44 (3.27)	100.21 ± .59 (3.86)	22.520 ± .097 (.712)	22.196 ± .122 (.871)
	2 yr.	♂♀	32	6	105	106.69 ± .59 (3.35)	102.15 ± 1.07 (4.80)	22.600 ± .154 (.871)	22.445 ± .217 (1.168)

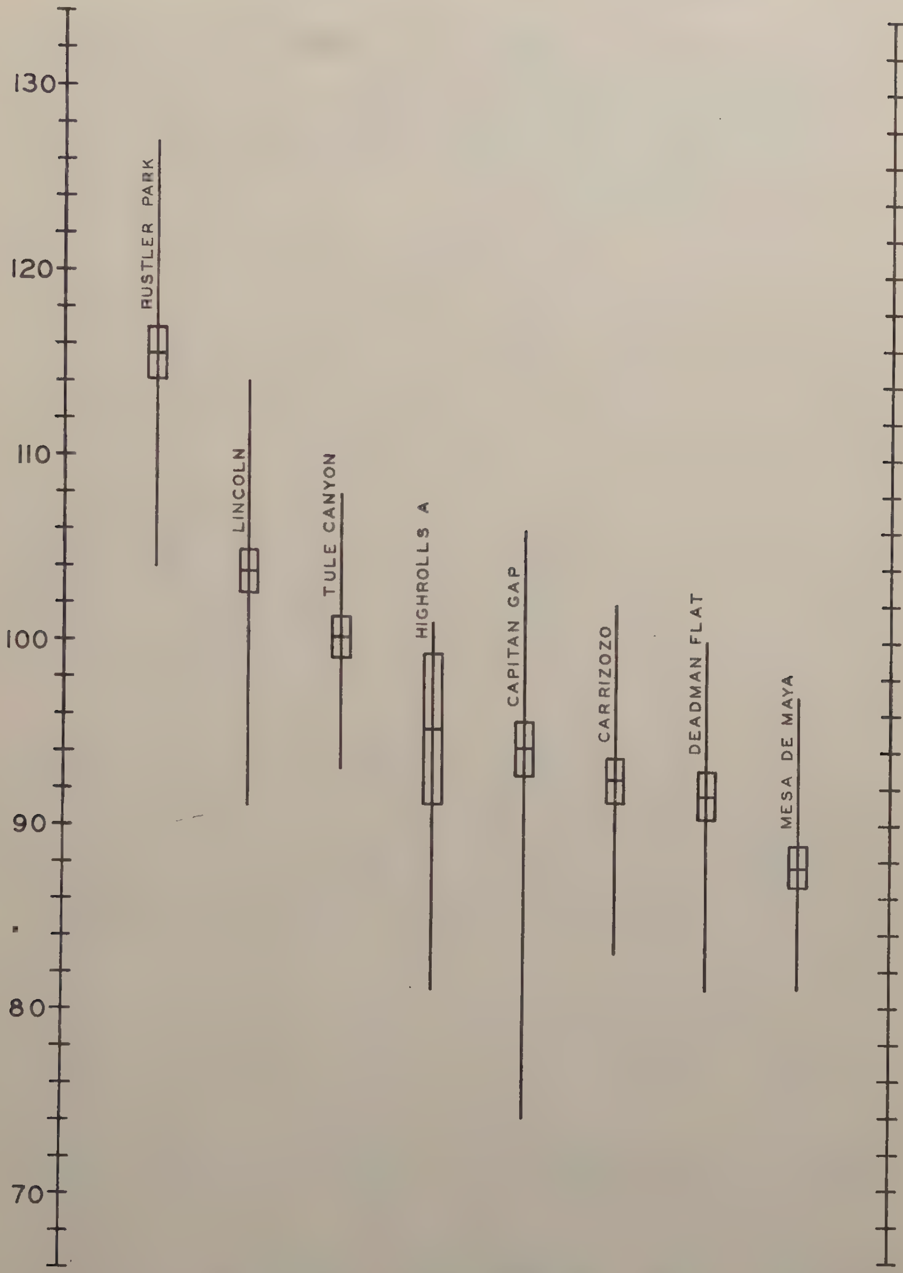


FIG. 1. Variation in tail length of laboratory-bred stocks of the Peromyscus truei group, shown by the graphical method of Dice and Leraas (1936). For each stock the length of the line represents the range in measurements, the rectangle indicates twice the standard error on each side of the mean, which is represented by the crossbar. In general, where rectangles do not overlap, the means differ significantly. One-year age class, both sexes.

exceeds in tail length the Capitan Gap, Carrizozo, and Deadman Flat stocks, but not the Highrolls A stock.

In length of hind foot there are relatively slight differences between the stocks. In the 1-year class the stock with the largest average hind foot (Deadman Flat) exceeds the stock with the smallest foot (Carrizozo) by only 1.419 mm.

In length of ear from notch there are conspicuous differences between the stocks. The Deadman Flat stock, with a mean of 26.197 mm for the 1-year class, significantly exceeds all the other stocks (Fig. 2). The Capitan Gap and Highrolls A stocks significantly exceed the Mesa de Maya stock, which in its turn significantly exceeds the Carrizozo, Lincoln, Tule Canyon, and Rustler Park stocks. The mean ear length of the Rustler Park stock, which averages the shortest in this measurement, is 21.981 mm.

In length of left femur the Capitan Gap stock, with a mean of 19.156 mm for the 1-year age class, significantly exceeded all the others (Table IV). The Deadman Flat, Rustler Park, and Lincoln stocks do not differ significantly from one another in this measurement, but they all significantly exceed the Highrolls A, Tule Canyon, and Mesa de Maya stocks. These 3 last stocks also do not differ significantly from one another, but they all significantly exceed the Carrizozo stock, which has a mean femur length of 17.412 mm.

Mandibular length differs only slightly among these 8 stocks, but some of the differences are of statistical significance. The Rustler Park stock, with a mean for the 1-year class of 17.942 mm, significantly exceeds all the other stocks. The Lincoln stock in its turn significantly exceeds in this measurement all but the Rustler Park stock. The Mesa de Maya stock, with a mean mandibular length of 16.458 mm, is significantly shorter in this character than any of the other stocks.

In condylo-premaxillary skull length the differences between the stocks are relatively slight. For the 1-year age class the mean for the Highrolls A stock, which is highest, is 27.811 mm, while for the Mesa de Maya stock, which is lowest, the skull length mean is 26.298 mm. The Mesa de Maya stock averages significantly shorter than all the other 7 stocks. None of the others fall into distinct size groups for this measurement.

The measurement of condylo-zygomatic distance also exhibits relatively slight variability among these eight stocks. The Highrolls A stock, with a mean for the 1-year age class of 19.989 mm, is highest and the Carrizozo stock, with a mean of 18.941 mm, is lowest.

In bullar width of skull the Highrolls A, Capitan Gap, and Rustler Park stocks do not differ significantly from one another, but all significantly exceed the other 5 stocks. The mean of the Highrolls A stock, which is highest of all, is 12.533 mm for the 1-year class, while the mean of the Carrizozo stock, which is lowest, is 12.068 mm.

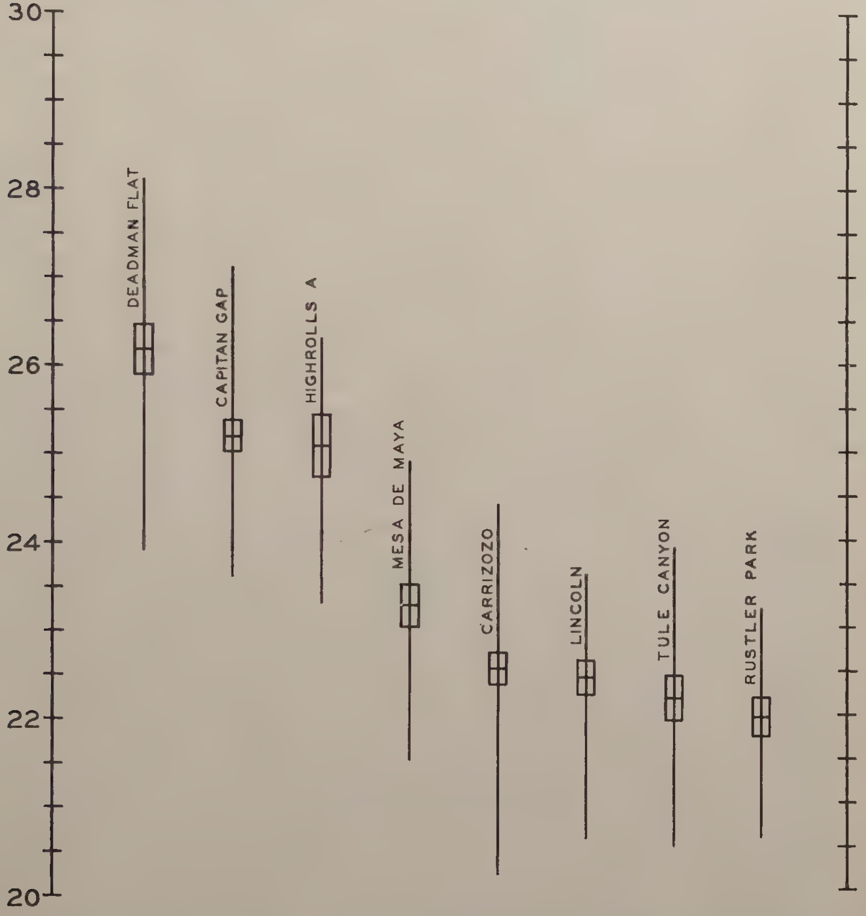


FIG. 2. Variation in ear length of laboratory-bred stocks of the Peromyscus truei group, shown by the same graphical method used in Figure 1. One-year age class, both sexes.

A small number of these animals were weighed at the time they were killed (Table V). The number of individuals weighed in each series is too small to serve as the basis for a reliable mean, in view of the considerable variation which occurs. The figures are presented here merely to show the average weight of laboratory-

TABLE IV

Measurements of the Peromyscus truei Group

Means, standard errors, and standard deviations are in millimeters.

Stock	Age Class	Sex	Femur Length	Mandible Length	Condyle-premaxilla Length	Condyle-zygoma Length	Bullar Width
truei							
Capitan Gap . .	1 yr.	♂♂	19.026 ± .106 (.592)	17.123 ± .047 (.259)	26.997 ± .087 (.475)	19.216 ± .058 (.322)	12.419 ± .042 (.232)
	1 yr.	♀♀	19.279 ± .130 (.745)	17.309 ± .067 (.388)	27.100 ± .092 (.534)	19.344 ± .069 (.404)	12.444 ± .046 (.269)
	1 yr.	♂+♀	19.156 ± .085 (.677)	17.220 ± .043 (.343)	27.052 ± .063 (.506)	19.283 ± .046 (.370)	12.432 ± .031 (.251)
Deadman Flat .	1 yr.	♂♂	18.444 ± .095 (.476)	17.292 ± .082 (.419)	26.992 ± .081 (.406)	19.140 ± .053 (.245)	12.195 ± .032 (.147)
	1 yr.	♀♀	18.410 ± .130 (.714)	17.145 ± .093 (.516)	26.936 ± .102 (.537)	19.066 ± .077 (.417)	12.210 ± .037 (.199)
	1 yr.	♂+♀	18.426 ± .083 (.612)	17.212 ± .063 (.476)	26.962 ± .065 (.476)	19.100 ± .048 (.353)	12.204 ± .025 (.177)
	2 yr.	♂+♀	18.417 ± .120 (.656)	17.466 ± .085 (.456)	27.180 ± .132 (.721)	19.303 ± .089 (.486)	12.217 ± .064 (.350)
Highrolls A . .	1 yr.	♂+♀	17.956 ± .075 (.319)	17.261 ± .082 (.348)	27.811 ± .125 (.529)	19.989 ± .080 (.339)	12.533 ± .047 (.200)
Mesa de Maya .	1 yr.	♂+♀	17.698 ± .077 (.554)	16.458 ± .064 (.477)	26.298 ± .066 (.482)	19.019 ± .044 (.325)	12.085 ± .021 (.155)
	2 yr.	♂+♀	18.566 ± .075 (.461)	17.174 ± .077 (.480)	27.082 ± .075 (.462)	19.462 ± .054 (.344)	12.251 ± .036 (.221)
nasutus							
Lincoln	1 yr.	♂+♀	18.234 ± .066 (.479)	17.562 ± .052 (.375)	27.266 ± .066 (.481)	19.374 ± .052 (.375)	12.206 ± .040 (.287)
Rustler Park .	1 yr.	♂+♀	18.291 ± .070 (.456)	17.942 ± .062 (.406)	27.438 ± .084 (.547)	19.248 ± .054 (.353)	12.386 ± .033 (.218)
	2 yr.	♂+♀	19.000 ± .105 (.547)	18.492 ± .107 (.547)	28.192 ± .113 (.575)	19.637 ± .077 (.400)	12.563 ± .052 (.268)
griseus							
Carrizozo . . .	1 yr.	♂+♀	17.412 ± .067 (.575)	17.075 ± .049 (.423)	26.689 ± .046 (.396)	18.941 ± .046 (.395)	12.068 ± .030 (.265)
	2 yr.	♂+♀	17.797 ± .160 (.876)	17.571 ± .097 (.542)	27.720 ± .164 (.899)	19.320 ± .124 (.677)	12.360 ± .043 (.236)
comanche							
Tule Canyon . .	1 yr.	♂+♀	17.900 ± .061 (.426)	16.898 ± .060 (.426)	26.620 ± .076 (.489)	18.962 ± .053 (.344)	12.124 ± .040 (.235)
	2 yr.	♂+♀	18.329 ± .129 (.684)	17.348 ± .100 (.538)	27.052 ± .133 (.714)	19.259 ± .094 (.508)	12.278 ± .060 (.314)

reared mice of the truei group. It will be noted that the mean weights center fairly closely around 30 grams.

TABLE V

Individual Weights in the Peromyscus truei Group

Means, standard errors, and standard deviations are in grams.

Stock	Age Class	Males		Females	
		Number	Mean ± S.E. (S.Dev.)	Number	Mean ± S.E. (S.D.)
truei					
Mesa de Maya	1 yr.	28	28.11 ± .61 (3.24)	28	26.46 ± .70 (3.73)
	2 yr.	16	32.21 ± 1.73 (6.93)	15	30.05 ± 1.71 (6.64)
Deadman Flat	1 yr.	16	35.81 ± 1.18 (4.71)	13	30.08 ± 1.64 (5.92)
nasutus					
Tule Canyon	1 yr.	16	31.81 ± 1.07 (4.30)	17	31.88 ± 1.44 (5.95)

In summary, the 8 stocks of the truei group which are here compared exhibit relatively slight differences in mean hind-foot length, and in the measurements of the skull. The most conspicuous variation among the stocks is in the length of the tail, which varies from a mean of 115.53 mm for the 1-year age class of the Rustler Park stock to a mean of only 87.79 mm for the Mesa de Maya stock. Considerable variation also is exhibited among the stocks in ear length and femur length.

VARIATION IN PELAGE COLOR

The Mesa de Maya stock is the palest in color of the 8 stocks of the truei group here compared. In reflection-meter readings of pelage color this stock ranks highest for all 3 color screens and for both the dorsal and side stripes (Table VI). For all the readings except reflected blue from the side, the Mesa de Maya stock averages significantly higher than any other stock.

The Deadman Flat, Lincoln, and Tule Canyon stocks form a group which is next to the Mesa de Maya stock in paleness of pelage as shown by the reflection meter readings (Fig. 3). The Capitan Gap stock does not have significantly lower readings than these for dorsal stripe red or side red, but for the other color comparisons it ranks below them.

The Carrizozo stock is significantly lower than any other stock in the color readings for dorsal-stripe red and dorsal-stripe green, and it does not average significantly higher than any other

TABLE VI

Reflection-meter Readings of the Pelage Color of the Peromyscus truei Group

Means, standard errors, and standard deviations of proportion of light reflected from the specimen are in comparison to that reflected from a magnesium carbonate block (taken as 100).

Stock	Age Class	Sex	DORSAL STRIPE			SIDE STRIPE		
			Red	Green	Blue	Red	Green	Blue
truei								
Capitan Gap . .	1 yr.	♂♂	17.85 ± .25 (1.59)	10.08 ± .12 (.74)	6.75 ± .10 (.63)	36.03 ± .56 (3.53)	20.55 ± .29 (1.83)	12.35 ± .17 (1.08)
	1 yr.	♀♀	17.45 ± .26 (1.59)	10.05 ± .12 (.73)	6.66 ± .11 (.67)	36.34 ± .44 (2.68)	19.13 ± .31 (1.88)	11.55 ± .21 (1.29)
	1 yr.	♂+♀	17.65 ± .18 (1.59)	10.06 ± .09 (.80)	6.71 ± .07 (.65)	36.18 ± .35 (3.13)	19.86 ± .22 (1.97)	11.96 ± .14 (1.24)
Deadman Flat .	1 yr.	♂♂	17.48 ± .57 (2.84)	9.92 ± .24 (1.19)	6.84 ± .18 (.90)	35.76 ± .77 (3.85)	20.96 ± .40 (2.01)	12.60 ± .19 (.96)
	1 yr.	♀♀	18.24 ± .28 (1.42)	10.28 ± .23 (1.17)	6.88 ± .16 (.78)	38.36 ± .88 (4.39)	20.52 ± .36 (1.81)	12.32 ± .27 (1.35)
	1 yr.	♂+♀	17.86 ± .32 (2.26)	10.08 ± .17 (1.18)	6.86 ± .12 (.83)	37.06 ± .61 (4.29)	20.74 ± .27 (1.90)	12.46 ± .17 (1.16)
	2 yr.	♂+♀	19.12 ± .39 (2.25)	10.06 ± .21 (1.22)	6.66 ± .14 (.78)	38.73 ± .40 (2.27)	20.91 ± .36 (2.07)	12.15 ± .24 (1.35)
Highrolls A . .	1 yr.	♂+♀	16.40 ± .29 (1.31)	9.40 ± .21 (.94)	6.25 ± .10 (.44)	33.55 ± .63 (2.82)	19.80 ± .47 (2.09)	11.25 ± .32 (1.41)
Mesa de Maya .	1 yr.	♂+♀	20.86 ± .29 (2.14)	13.00 ± .18 (1.34)	8.70 ± .13 (.97)	40.52 ± .63 (4.73)	23.64 ± .28 (2.12)	14.02 ± .16 (1.21)
	2 yr.	♂+♀	19.88 ± .42 (2.63)	12.35 ± .29 (1.83)	8.55 ± .20 (1.26)	41.38 ± .77 (4.89)	24.58 ± .39 (2.48)	14.20 ± .26 (1.64)
nasutus								
Lincoln	1 yr.	♂+♀	17.75 ± .26 (1.99)	11.39 ± .15 (1.13)	7.81 ± .10 (.77)	34.00 ± .47 (3.55)	21.68 ± .25 (1.90)	13.65 ± .21 (1.60)
Rustler Park .	1 yr.	♂+♀	15.45 ± .19 (1.34)	9.72 ± .14 (1.01)	6.51 ± .09 (.65)	29.55 ± .33 (2.34)	17.43 ± .19 (1.32)	10.69 ± .15 (1.07)
	2 yr.	♂+♀	15.63 ± .24 (1.44)	9.57 ± .15 ((.88)	6.34 ± .11 (.64)	30.17 ± .43 (2.54)	17.60 ± .32 (1.91)	10.57 ± .17 (.98)
griseus								
Carrizozo. . .	1 yr.	♂+♀	13.00 ± .23 (2.11)	7.64 ± .14 (1.25)	5.93 ± .09 (.85)	28.22 ± .46 (4.12)	17.63 ± .25 (2.28)	11.98 ± .17 (1.51)
	2 yr.	♂+♀	11.94 ± .38 (2.15)	7.16 ± .21 (1.17)	5.75 ± .11 ((.62)	28.03 ± .55 (3.09)	17.19 ± .39 (2.22)	11.84 ± .26 (1.46)
comanche								
Tule Canyon. .	1 yr.	♂+♀	17.54 ± .23 (1.66)	11.06 ± .13 (.92)	7.22 ± .11 (.77)	36.83 ± .51 (3.71)	21.76 ± .28 (2.06)	13.13 ± .21 (1.52)
	2 yr.	♂+♀	17.20 ± .38 (1.89)	10.56 ± .20 (1.00)	6.76 ± .16 (.78)	38.64 ± .86 (4.28)	23.08 ± .44 (2.22)	13.48 ± .25 (1.26)

stock except for side-stripe blue, in which it significantly exceeds the Rustler Park stock.

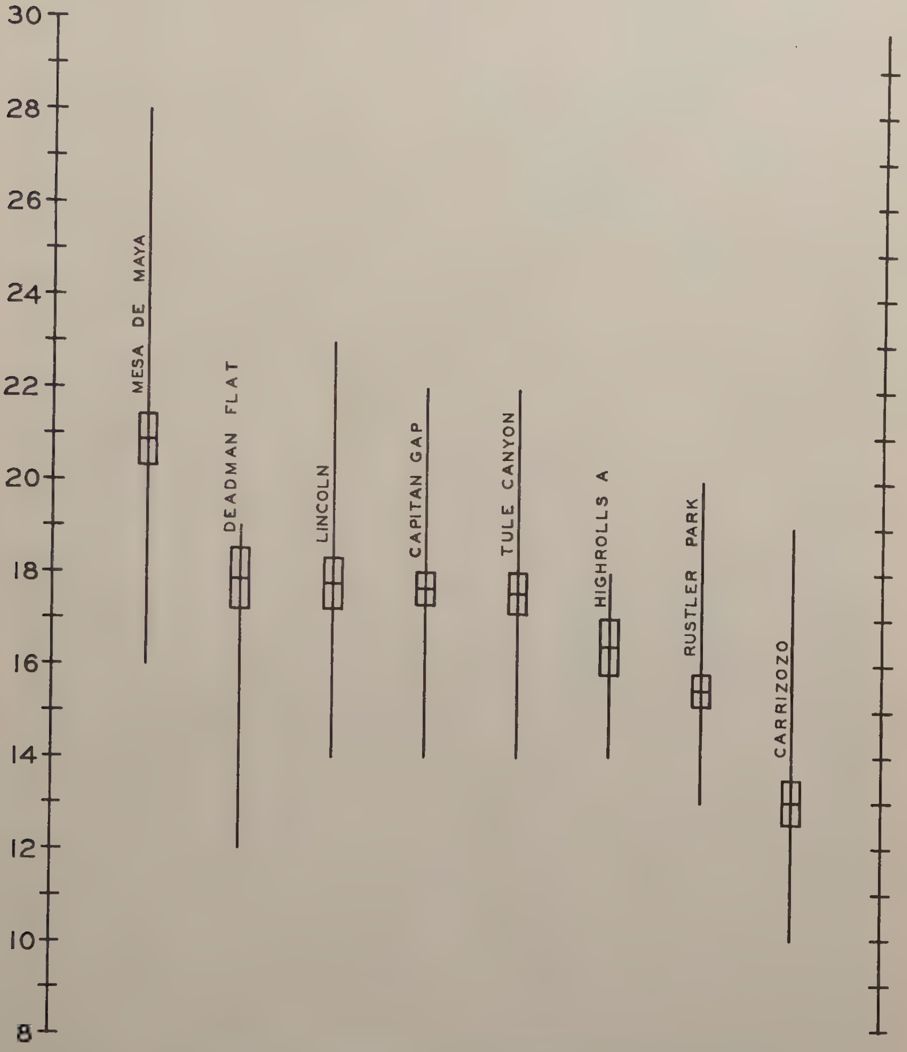


FIG. 3. Variation in reflection-meter readings of reflected red from the dorsal stripe of specimens prepared from laboratory-bred stocks of the Peromyscus truei group, shown by the same graphical method used in Figure 1. One-year age class, both sexes.

The Rustler Park and Highrolls A stocks rank in general just above the Carrizozo stock in color readings, except for blue reflected from the side stripe, for which the Rustler Park stock ranks significantly below the Carrizozo stock.

It may be said, therefore, that of the 8 stocks of the truei group here compared, the stock from Mesa de Maya is the palest and that from Carrizozo is the darkest. The other stocks are intermediate in shade of color. The Deadman Flat, Lincoln, and Tule Canyon stocks are relatively pale and are exceeded in color readings of reflected light only by the Mesa de Maya stock. The Capitan Gap stock ranks slightly darker than these 3 stocks for certain colors. The Rustler Park and Highrolls A stocks are relatively dark, and they rank immediately above the Carrizozo stock in reflection-meter readings.

The pelage colors of these stocks, however, form a fairly evenly graded series. No one of them is clearly distinct from the others in shade of color. The Mesa de Maya stock appears to be most distinct, but many of the individuals of this stock cannot be distinguished in color readings from certain individuals of the other stocks.

No differences in hue between these stocks are apparent. The pigments concerned in producing the pelage colors are believed to be the same in all the stocks, although no microscopic examinations have been made of the hairs.

The relatively dark pelage of the Carrizozo mice is evidently correlated with the black color of the lava soil in the habitat of the subspecies griseus (Bradt, 1932; Benson, 1933; Dice and Blossom, 1937). Likewise the pale color of the Mesa de Maya mice may be presumed to be correlated with the pale color of the rocks of the xeric habitat where the female ancestor of this stock was taken. Museum skins of several other truei collected at the same place are similarly pale. The ancestors of the other stocks which are here described came from habitats in which the surface soils are intermediate in shade between the Malpais and Mesa de Maya soils. No soil samples were collected from most of these habitats, however, and no critical comparison can be made between the pelage color of the mice and the color of the soils of their habitats.

Most of the color measurements given in this paper were taken with a Photovolt reflection meter. These measurements are not directly comparable with those taken with the Hess-Ives tint photometer and published in earlier papers dealing with variation in Peromyscus. For comparison with the readings taken with the tint photometer and previously published, I here present tint-photometer readings of pelage color for a few of these stocks (Table VII).

Both the reflection meter and the tint photometer use color filters to produce red, green, and blue readings, but the wave lengths passed by the filters and the percentage of light transmission

TABLE VII

Tint-photometer Readings of the Pelage Color of Certain Stocks of the Peromyscus truei Group

Means, standard errors, and standard deviations of proportion of light reflected from the specimen are in comparison to that reflected from a magnesium carbonate block (taken as 100). Measurements of males and females are combined.

Stock	Age Class	DORSAL STRIPE			SIDE STRIPE		
		Red	Green	Blue	Red	Green	Blue
truei							
Capitan Gap . . .	1 yr.	15.87 ± .21 (1.84)	11.89 ± .15 (1.35)	9.28 ± .12 (1.01)	26.55 ± .27 (2.37)	19.51 ± .21 (1.81)	14.55 ± .21 (1.89)
Deadman Flat . .	1 yr.	15.79 ± .23 (1.61)	12.25 ± .19 (1.28)	9.63 ± .17 (1.16)	25.83 ± .41 (2.82)	19.04 ± .31 (2.14)	14.38 ± .30 (2.09)
	2 yr.	14.15 ± .63 (3.64)	10.58 ± .43 (2.47)	8.27 ± .32 (1.83)	24.24 ± .91 (5.21)	17.70 ± .68 (3.90)	13.67 ± .57 (3.27)
Highrolls A . . .	1 yr.	10.60 ± .29 (1.29)	8.30 ± .29 (1.30)	5.95 ± .22 (1.00)	19.70 ± .41 (1.81)	14.25 ± .32 (1.41)	9.90 ± .33 (1.48)
Mesa de Maya . .	1 yr.	15.34 ± .39 (2.89)	12.18 ± .32 (2.40)	9.43 ± .28 (2.11)	27.84 ± .50 (3.75)	20.63 ± .37 (2.75)	14.88 ± .29 (2.17)
	2 yr.	12.90 ± .35 (2.20)	10.00 ± .26 (1.63)	7.88 ± .19 (1.19)	26.55 ± .61 (3.83)	20.03 ± .44 (2.75)	13.90 ± .32 (2.02)

TABLE VIII

Reflection-meter Readings of Pelage Color of Hybrids between Various Members of the Peromyscus truei group and of P. n. griseus from Carrizozo

Means, standard errors, and standard deviations of amount of light reflected from the specimens are in comparison to that reflected from a magnesium block (taken to be 100). Males and females are taken together.

Stock Mated with griseus	Generation	Age Class	Number	DORSAL STRIPE			SIDE STRIPE		
				Red	Green	Blue	Red	Green	Blue
Rustler Park									
nasutus	F_1	2 yr.	11	12.27 ± .47 (1.56)	8.18 ± .30 (.98)	6.00 ± .23 (.78)	27.91 ± .90 (2.98)	17.36 ± .56 (1.86)	11.73 ± .49 (1.62)
	F_2	1 yr.	41	12.88 ± .31 (1.93)	7.95 ± .19 (1.18)	6.32 ± .13 (.82)	27.22 ± .49 (3.09)	16.78 ± .31 ((1.93)	11.46 ± .18 (1.14)
Lincoln									
nasutus	F_1	2 yr.	17	12.53 ± .36 (1.46)	7.47 ± .19 (.80)	6.59 ± .05 (.20)	29.35 ± 1.24 (5.12)	17.47 ± .59 (2.43)	12.35 ± .32 (1.32)
	F_2	1 yr.	35	11.43 ± .24 (1.42)	7.09 ± .19 (1.15)	5.97 ± .38 (2.23)	25.51 ± .63 (3.71)	16.37 ± .35 (2.06)	11.74 ± .24 (1.44)
Deadman Flat									
truei	F_1	1+2 yrs.	16	15.63 ± .60 (2.39)	9.19 ± .39 (1.56)	6.56 ± .33 (1.32)	34.81 ± 1.09 (4.34)	19.56 ± .49 (1.97)	12.25 ± .30 (1.18)

differ for the 2 instruments. In general, the tint photometer gives lower readings than the reflection meter. It would be futile, however, to attempt to compare the readings of the 2 instruments in any quantitative manner.

PELAGE COLOR OF HYBRIDS

Measurements of pelage color are available for a few hybrids of griseus from Carrizozo with other stocks of the truei group (Table VIII). Both the F_1 and F_2 hybrids of crosses of griseus with nasutus from Rustler Park and from Lincoln have color readings which are close to griseus. In a cross with truei from Deadman Flat, however, the F_1 hybrids are more or less intermediate in color readings between the 2 parent stocks. The standard errors of the means are fairly high for most of these pelage color readings of the hybrids, and it seems unwise to attempt to draw any conclusions from these data about the mode of heredity of the dark pelage of griseus.

FERTILITY RELATIONS

Crosses in the laboratory between stocks of the subspecies Peromyscus truei truei taken in various parts of its geographic range have all been at least moderately successful. The F_1 hybrid males and females, so far as they have been tested, have all proved to be fertile (Dice, 1933b; Dice and Liebe, 1937). Crosses between diverse stocks from within the range of the subspecies Peromyscus nasutus nasutus have also been successfully made in the laboratory, and both the male and female F_1 hybrids seem to be as fertile as the mice of the parent stocks.

In addition to the intrasubspecific crosses of nasutus previously reported, I have successfully crossed a stock from Rustler Park in the Chiricahua Mountains of Arizona with individuals of the same subspecies from stations B, C, and E near Highrolls, New Mexico. The Rustler Park stock has also been crossed with a stock of the same subspecies from Lincoln, New Mexico. No difficulty has been encountered in securing the F_2 generation in any of these crosses between stocks of the same subspecies.

Various subspecies of the same species within the truei group have also been successfully crossed in the laboratory. Thus, the 2 subspecies Peromyscus truei truei and P. t. gilberti have crossed in the laboratory and have produced young (Dice, 1933b). The fertility of these F_1 hybrids was not tested, but presumably they would have been fertile. In the species nasutus, the subspecies griseus from near Carrizozo, New Mexico, has been crossed with nasutus from Rustler Park and also with nasutus from Lincoln. In these crosses both the male and the female F_1 hybrids proved to be fertile.

Within any single species of this group of mice, consequently, all the individuals seem to be potentially interfertile, whether or not they are members of the same subspecies and irrespective of the geographic distance that may separate their habitats.

In crosses between species in this group of mice, however, we encounter partial infertility. Peromyscus truei truei and P. nasutus griseus will cross in the laboratory and most of their F_1 female offspring are fertile. The hybrid males, on the contrary, are uniformly infertile and no viable spermatozoa were found (Dice and Liebe, 1937).

In addition to the hybrids between these species previously reported, I have crossed a stock of nasutus from Rustler Park with a stock of truei from Deadman Flat. Of 21 matings only 3 were fertile. Ten hybrid young were reared to weaning age, though others were born that did not survive. Of these 10 F_1 hybrids, 5 were females and 5 males. Of the F_1 hybrid females, one produced no offspring when backcrossed to a nasutus male, but did produce 7 young when backcrossed to a truei male. Another F_1 female produced 2 offspring from a backcross to a truei male. A third female produced no offspring when mated to a truei male. The other 2 females were not tested for fertility. All the F_1 males were infertile in backcrosses, 3 of them being tested with truei females and 2 with nasutus females.

The species Peromyscus comanche from Tule Canyon, Texas, will cross, though with some difficulty, with P. nasutus nasutus from Arizona and from New Mexico. One of 6 F_1 males from such crosses produced young when mated to a comanche female. The other 5 hybrid males produced no offspring, but from examination of their sperm one of them may have been potentially fertile (Blair, 1943).

No attempted crosses between either truei, nasutus, or nasutus with Peromyscus of any other species-group have ever been successful (Dice, 1933b). The evidence, therefore, indicates that the Peromyscus truei group is reproductively isolated from all the other mice of the genus Peromyscus. Within the truei group the 3 species comanche, nasutus, and truei are partly infertile with one another, this being shown particularly by the partial or complete infertility of the hybrid males. The several subspecies and local populations within each of these species, however, seem to be completely interfertile with one another.

SYSTEMATICS

Of the stocks here described, those from Capitan Gap, Deadman Flat, Highrolls A, and Mesa de Maya may be assigned to the species truei on the basis of their size of ear (Fig. 2). The Rustler Park and Lincoln stocks are assigned to nasutus.

Nasutus not only has a smaller ear than truei, but it also has a longer tail. There are, however, considerable differences both in length of ear and of length of tail among the stocks assigned to truei and also among those assigned to nasutus. In addition, the individual variability within the stocks would make it impossible to assign every individual correctly to species on the basis of either ear size or tail length alone.

The Tule Canyon stock is assigned to the species comanche, which in length of ear is closer to the species nasutus than to truei. Breeding tests, however, indicate that comanche is partly infertile in crosses with nasutus (Blair, 1943). No breeding tests have been made with truei. In tail length comanche is closer to truei than to nasutus.

The Carrizozo stock is assigned to the subspecies griseus of the species nasutus. The ears of the mice of this stock are similar in size to those of nasutus and are strikingly smaller than those of truei. The tail averages shorter, however, than in the other stocks of the species nasutus here described and does not differ significantly in length from the tails of the Highrolls, Capitan Gap, and Deadman Flat stocks of undoubted truei. In its fertility relations, griseus is clearly differentiated from truei and is closely related to nasutus.

The evidence seems to indicate clearly that griseus is a subspecies of nasutus not yet sufficiently differentiated to have become even partly infertile when backcrossed. Nevertheless, griseus differs strikingly from nasutus in its shorter length of tail and in its darker pelage color. This demonstrates again that the body proportions and pelage color of mammals often rapidly become modified in the course of evolution.

The occurrence together in the same region and often in the same local habitats of the 2 species truei and nasutus (Dice, 1942) is of especial interest to the student of evolution. These 2 species are closely related and are assigned to the same species group of the subgenus Peromyscus. They are sufficiently closely related so that hybrids can be obtained in the laboratory, although no hybrids have ever been discovered in nature. The partial infertility which exists between the 2 forms is probably sufficient to retain the distinctness between them, even if occasional interbreeding should occur in those situations where both forms occur. It seems probable that miscegenation rarely if ever occurs. So far as I know, no laboratory studies of assortative mating between the 2 forms have been carried out, but it is likely that each form prefers to mate with its own kind.

From what is now known about the conditions under which new species originate through the splitting of an ancestral form, some form of isolation must initially have separated certain of the local populations of the ancestor (Dobzhansky, 1941; Mayr, 1942). Isolation between nasutus and truei must be assumed to have continued for a sufficiently long period of time to result in the development of partial intersterility between the isolated populations. Subsequent to the development of partial infertility, these 2 forms have come to occupy broadly overlapping geographic ranges and habitats.

The pinyon and juniper habitats, in which the 2 species nasutus and truei most frequently live in southwestern North America, are often discontinuous in their distribution. The buttes and small mountain ranges which carry belts of pinyon pines and junipers often are isolated from one another by many miles of desert or grassland habitat inhospitable for the mice of this group. One such isolated butte or mountain range may be occupied by one or other only of these 2 species. In certain places both species occur together. Changes in the climate of the area over past ages have undoubtedly led to frequent changes in the distribution of habitats suitable for these mice, with consequent changes in the degree of isolation between adjacent sites. Abundant opportunities have consequently occurred in the past and still exist for the temporary isolation of small populations of these mice (Dice, 1940: 295).

The species comanche is geographically isolated from both nasutus and truei. It is known to be partly infertile with nasutus. The development of this partial infertility between comanche and nasutus may be presumed to be in considerable part a resultant of its isolation. The conditions of geographic isolation under which comanche has become differentiated from other members of the truei group may be presumed to illustrate the conditions under which at some time in the past, the species truei and nasutus likewise became differentiated from one another.

SUMMARY

Measurements are given of body and skeletal dimensions and of pelage color for 8 laboratory-bred stocks of the Peromyscus truei group of small rodents from the southwestern United States.

Two-year old animals average slightly larger than 1-year old in all body and skeletal measurements except hind-foot length. There is no significant difference in pelage color between the age classes.

Males and females do not differ significantly in any body or skeletal dimension or in pelage color.

Four of the stocks here described are assigned to Peromyscus truei truei, 2 to P. nasutus nasutus, 1 to P. nasutus griseus, and 1 to P. comanche. Nasutus has a shorter ear and a longer tail than truei. Griseus agrees with nasutus in having a relatively short ear, but in tail length it does not differ significantly from truei. Comanche also has a short ear, like nasutus, and a relatively short tail, like truei.

All the stocks of the same species within the truei group which have been tested are fully interfertile and both the male and female F_1 hybrids are fertile. Crosses between species within the truei group, on the contrary, are relatively infertile and the male F_1 hybrids are partly or completely sterile. No cross of a member of the truei group with any other species group has been successful.

The geographic distribution of the mice of the truei group is discontinuous over southwestern North America, because of the discontinuity of suitable habitats. The resulting isolation between the populations and their consequent independent evolution is believed to have been responsible for the origin of the diversity of forms of this group of small rodents represented in the region. The infertility between the species is assumed also to have resulted from long-continued isolation. At the present time the geographic ranges of the species truei and nasutus overlap and both species may live together in the same habitat without interbreeding.

LITERATURE CITED

BENSON, SETH B.

1933 Concealing coloration among some desert rodents of the southwestern United States. Univ. Calif. Publ. Zool., 40: 1-70.

BLAIR, W. FRANK

1943 Biological and morphological distinctness of a previously undescribed species of the Peromyscus truei group from Texas. Contrib. Lab. Vert. Biol. Univ. Mich., 24: 1-8.

BRADT, G. W.

1932 The mammals of the Malpais, an area of black lava rock in the Tularosa Basin, New Mexico. Journ. Mammal., 13: 321-28.

DICE, LEE R.

1930 Mammal distribution in the Alamogordo region, New Mexico. Occ. Papers Mus. Zool. Univ. Mich., 213: 1-32.

1932 Variation in a geographic race of the deer-mouse, Peromyscus maniculatus bairdii. Ibid., 239: 1-26.

1933a Variation in Peromyscus maniculatus rufinus from Colorado and New Mexico. Ibid., 271: 1-32.

1933b Fertility relationships between some of the species and subspecies of mice in the genus Peromyscus. Journ. Mammal., 14: 298-305.

1937 Variation in the wood-mouse, Peromyscus leucopus noveboracensis, in the northeastern United States. Occ. Papers Mus. Zool. Univ. Mich., 352: 1-32.

1939 Variation in the cactus-mouse, Peromyscus eremicus. Contrib. Lab. Vert. Gen. Univ. Mich., 8: 1-27.

1940 Speciation in Peromyscus. Amer. Nat., 74: 289-98.

1942 Ecological distribution of Peromyscus and Neotoma in parts of southern New Mexico. Ecology, 23: 199-208.

1947 Effectiveness of selection by owls of deer-mice (Peromyscus maniculatus) which contrast in color with their background. Contrib. Lab. Vert. Biol. Univ. Mich., 34: 1-20.

DICE, LEE R., and PHILIP M. BLOSSOM

1937 Studies of mammalian ecology in southwestern North America, with special attention to the colors of desert mammals. Publ. Carnegie Instit. Wash., 485: 1-129.

DICE, LEE R., and HAROLD J. LERAAS

1936 A graphic method for comparing several sets of measurements. Contrib. Lab. Vert. Gen. Univ. Mich., 3: 1-3.

DICE, LEE R., and MARGARET LIEBE

1937 Partial infertility between two members of the Peromyscus truei group of mice. Contrib. Lab. Vert. Gen. Univ. Mich., 5: 1-4.

DOBZHANSKY, THEODOSIUS

1941 Genetics and the origin of species. 2nd ed.; New York: Columbia University Press.

HAYNE, DON W.

1950 Reliability of laboratory-bred stocks as samples of wild populations, as shown in a study of the variation of Peromyscus polionotus in parts of Florida and Alabama. Contrib. Lab. Vert. Biol. Univ. Mich., 46: 1-56.

HOFFMEISTER, DONALD F.

1951 A taxonomic and evolutionary study of the piñon mouse, Peromyscus truei. Illinois Biol. Monogr., 21 (No. 4): i-ix, 1-104.

MAYR, ERNST

1942 Systematics and the origin of species, from the viewpoint of a zoologist. New York: Columbia University Press.

SUMNER, FRANCIS B.

1926 An analysis of geographic variation in mice of the Peromyscus polionotus group from Florida and Alabama. Journ. Mammal., 7: 149-84.

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price, $0.30.

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

University of Michigan, Ann Arbor, Michigan

Number 58 June, 1952

WATER REQUIREMENTS OF CERTAIN RODENTS FROM XERIC AND MESIC HABITATS

By ROBERT G. LINDEBORG

Accepted for publication March 7, 1952

CONTENTS

Introduction 1
Stocks of Animals 2
Habitats of Forms 3
Laboratory Conditions 7
Water Consumption by Nonbreeding Adult Mice 7
Effects of Deficient Water Ration on Body Weight and Survival 12
Differences in Water Requirements of Mice from Humid and
from Xeric Habitats 23
Summary 28
Literature Cited 30

INTRODUCTION

MOST mammals require a daily supply of free water, although some desert forms are capable of existing with no source of water except that obtained from their food. The amount of water available in the habitats of the various kinds of mammals varies considerably. Furthermore, in certain seasons of the year, and especially in times of drought, the water available in certain habitats may be materially reduced. The water requirements of most forms undoubtedly are flexible enough to enable at least a part of each population to survive adverse periods. It is also to be expected that each form inhabiting a given region would have other adaptations related to water requirements which will enable it to survive any seasonal deficiency of the water supply.

This paper is concerned with two points: (1) the average water consumption of certain small rodents inhabiting xeric and moderately mesic climates, respectively, and (2) the ability of certain kinds of these rodents to survive a period of deficient water supply. The results of the experiments used to test these points are summarized in the present report; detailed records may be obtained from Lindeborg (1948).

I express my gratitude to Dr. Lee R. Dice of the University of Michigan for supervising my work and to Dr. W. F. Blair for many suggestions. To Dr. C. W. Cotterman, Dr. C. C. Craig, and Dr. Leo Katz, I am indebted for aid with the statistical analysis. The Laboratory of Vertebrate Biology of the University of Michigan supplied most of the equipment and stocks of mice. The completion of the study was supported in part by the Biological Science Department of Michigan State College, and Dr. H. R. Hunt of the Zoology Department of that college graciously furnished laboratory space.

STOCKS OF ANIMALS

The several stocks of mice used in this study were secured at different times by L. R. Dice, W. F. Blair, W. H. Burt, M. A. Taylor, B. T. Ostenson, P. R. Sime, M. F. Landwer, and R. G. Lindeborg. The expeditions on which the stocks were collected were supported in part by the Carnegie Institution of Washington and in part by the Laboratory of Vertebrate Biology, the Museum of Zoology, and the Horace H. Rackham School of Graduate Studies of the University of Michigan.

The species and races of mice upon which observations were made are listed below. Scientific names are those of Miller (1923) unless otherwise stated.

Perognathus penicillatus eremicus. — Field-caught animals collected about 3 miles south of Alamogordo, Otero County, New Mexico.

Peromyscus eremicus eremicus. — Three stocks of laboratory-bred animals were tested. The mice used in the water-consumption determination of the eremicus — blandus series were collected near Lone Butte, about 13 miles west of Tularosa, Otero County, New Mexico. The mice utilized for a similar determination (Table II, Series 8) were collected 3 miles south of Alamogordo, Otero County, New Mexico. The stock tested in the water-deficiency experiment was collected 13 miles west of Oscuro, Lincoln County, New Mexico.

Peromyscus maniculatus gracilis. — The three stocks were collected in the Upper Peninsula of Michigan. Two of these originated in the Cusino State Game Area, Alger County: one stock was field-caught, the other laboratory-bred. The third stock, also field-caught, was collected near the town of Norway, Dickinson County, about 65 miles southwest of the Cusino area.

Peromyscus maniculatus rufinus. — Laboratory-bred animals. The parent stock was collected on the north side of Gyp Spring Canyon, 4 miles northeast of Capitan, Lincoln County, New Mexico.

Peromyscus maniculatus nebrascensis. — Laboratory-bred animals. The original stock was collected near Kennedy, 40 miles south of Valentine, Cherry County, Nebraska.

Peromyscus maniculatus bairdi. — Laboratory-bred mice. The parent stock was collected about 5 miles southwest of Fennville, Allegan County, Michigan.

Peromyscus maniculatus blandus. — Laboratory-bred mice. The original stock was taken about 3 miles south of Alamogordo, Otero County, New Mexico.

Peromyscus maniculatus exiguus (see Nelson and Goldman, 1932). — Laboratory-bred animals. The original stock was collected on San Martín Island, about 3 miles off the coast of Baja California (30° 29' N: 116° 07' W).

Peromyscus leucopus noveboracensis. — Field-caught animals from southern Michigan. Most of these were collected near Pinckney, Livingston County, but a few were taken near Ann Arbor, Washtenaw County.

Peromyscus leucopus tornillo. — Field-caught animals collected about 2 miles southwest of Alamogordo, Otero County, New Mexico.

Peromyscus truei truei. — Laboratory-bred mice. The original stock was trapped at Capitan Gap about 6 miles northeast of Capitan, Lincoln County, New Mexico.

Peromyscus comanche Blair (1943c). — The parent stock was collected on the slopes of Tule Canyon, about 12 miles northeast of Silvertown, Briscoe County, Texas (Panhandle section).

Microtus pennsylvanicus pennsylvanicus. — Field-caught voles trapped near Ann Arbor, Washtenaw County, Michigan.

HABITATS OF FORMS

Most of the stocks of mice employed in this investigation live under one of two contrasting types of climate: (1) the semidesert climate of southern New Mexico and (2) the deciduous-forest-and-prairie climate of southern Michigan. Meteorological data for these two climatic types are summarized in Table I.

TABLE I

Meteorological Summaries for Alamogordo, New Mexico,
and for Ann Arbor, Michigan

From the United States Weather Bureau "Climatic Summary of the United States."

	Alamogordo	Ann Arbor
Precipitation (in inches)		
Mean annual	10.92	31.35
Months with more than one inch of rain	4	12
Months with less than one inch of rain	8	0
Months with more than two inches of rain	0	10
Temperature (Fahrenheit)		
Mean annual	61°	47°
Lowest monthly mean temperature	41.8°	22.6°
Highest monthly mean temperature	79.7°	71.7°
Mean annual relative humidity (approximate)	45%	75%
Mean annual total snow (in inches)	5.8	37.4

Southern New Mexico, in the region of Alamogordo, is characterized by slight precipitation, most of which falls in late summer. The 4 months with more than 1 inch of rain are July, August, September, and October. Periods of 70 consecutive days with less than 0.25 of an inch of rain may occur from March through September (Kincer, 1922). During 19 years, more than 30 periods of 30 consecutive days with less than 0.25 of an inch of rain have occurred.

In comparison with southern New Mexico, southern Michigan has a greater annual precipitation, which is evenly distributed throughout the year. Southern Michigan also has a lower mean annual temperature and a higher mean annual relative humidity. The 2 months with less than 2 inches of precipitation are January and February. Periods of from 42 to 49 consecutive days with less than 0.25 of an inch of rain have been known to occur between March and September, but in 19 years there have been only 12 periods of 30 consecutive days in which less than 0.25 of an inch of rain was recorded.

The types of vegetation that have developed under these 2 climatic regimes are also quite distinctive. The vegetation of southern New Mexico is sparse and xerophytic, except for the mountainous regions, which are forested. Dice (1942) subdivides the area into 4 major belts: the montane belt, the sabinal belt, the arid grassland belt, and the desert belt. The montane belt is discontinuous on mountain tops, where the characteristic tree is the yellow pine (Pinus ponderosa). The lower regions of this belt are made up of juniper and oak and are assigned to the oak-brush association. Below the montane belt is the sabinal belt, characterized mainly by the pinyon pine (Pinus edulis) and the sabino juniper (Juniperus monosperma). Along the sides of canyons and valleys a rocky-slope association frequently occurs, and the borders of the more permanent streams are assigned to the nogale association characterized by the nogale or walnut (Juglans major). A treeless area is frequent on the eastern slopes of the mountains and has been called the short-grass association. The arid grassland belt is at a lower level. It is missing on the western slopes of the Sacramento Mountains, where the desert belt extends upwards to meet the sabinal belt. The desert belt is at lower elevations and includes the desert plain and the lower desert slopes of the adjacent mountains. Four subdivisions of the desert plains are recognized in this area by Blair (1943a). Three of these (the creosote bush, mesquite, and atriplex associations) occupy broad belts lying parallel to the mountain front and are encountered in that order as one proceeds from the base of the mountains to the center of the Tularosa Basin. The fourth subdivision, the grassy-wash association, cuts across the other associations of the desert plain.

The vegetation of southern Michigan is largely mesophytic with a number of hydrophytic forms. The 2 main physiognomic types, grassland and forest, are discontinuous. Forested areas at ground level have slightly lower temperature, higher humidity, lower evaporation, less insolation, and less air movement than nonforested areas.

Five races of Peromyscus and one of Perognathus from the New Mexico area were tested. Descriptions of the areas where the mice were trapped are to be found in Dice (1930, 1940, and 1942) and Blair (1941, 1943a and 1943b). Peromyscus maniculatus rufinus is typical of the montane belt but occasionally it ranges also through the sabinal belt, avoiding the rocky slopes, and into the arid grassland. Peromyscus truei truei is most abundant among the rocks and cliffs in the sabinal belt; it ranges upwards into the rocky habitats of the yellow-pine association of the montane belt and sometimes extends down into the desert belt, where it has been taken with Peromyscus maniculatus blandus in the mesquite association and with P. leucopus tornillo in the grassy washes. Peromyscus eremicus eremicus lives mostly in rocky habitats of the desert and grassland belts. This species is associated with P. m. blandus in the mesquite and with P. l. tornillo (Blair, 1943a) in the grassy washes. Peromyscus maniculatus blandus inhabits a number of areas on the desert plains, but occurs in greatest abundance in the mesquite association and only rarely in the creosote bush and atriplex areas. This race ranges into the grassy washes, where it is found with P. leucopus tornillo. Tornillo is found characteristically in these washes but ranges occasionally into the mesquite and into the nogale associations. In the desert belt it seems to prefer the less arid habitats. Perognathus penicillatus eremicus is widely distributed on the desert plains and is most abundant in the mesquite, where it was taken with Peromyscus maniculatus blandus, and it is almost as abundant in the creosote-bush association, but uncommon in desert washes.

Peromyscus leucopus noveboracensis, P. maniculatus bairdi and one race of Microtus tested inhabit southern Michigan. P. l. noveboracensis, chosen to contrast with P. l. tornillo from New Mexico, lives in areas which are wooded or covered with heavy brush; certain individuals, however, have been taken several hundred yards from the woods in open grassland (Burt, 1940). P. m. bairdi, selected for comparison with P. m. blandus from New Mexico, is always found in well-drained open places, in fields, meadows, and pastures; it is especially abundant in the thickly matted and undisturbed grass along fence rows. It occurs sometimes in fields containing scattered shrubs but never in forests or thick brush. In fact, there is some evidence that its home ranges rarely if ever reach the edges of woods (Blair, 1940). Microtus pennsylvanicus pennsylvanicus occupies the poorly drained grasslands, meadows, and marshes. It is partial to moist ground and prefers rough meadows, where the grass is matted and dense, but may extend its range to higher ground during favorable conditions, receding again during dry weather.

Four other races of Peromyscus, representing several additional habitats were also tested. P. maniculatus gracilis occupies the same general habitats as P. l. noveboracensis, but in Michigan is confined to the northern part of the state. It is also found at times in open places, and commonly invades barns and hunting cabins and occasionally farm houses. P. m. nebrascensis is largely limited to the Sand Hills of western Nebraska. Precipitation in this area averages 23 inches per year, a status intermediate between the Alamogordo and Ann Arbor regions. The soil is loose and sandy with very little surface drainage. Surface soil is commonly dry as powder, but beneath the surface it is quite moist (Pool, 1912). The vegetation is sparse and characterized by bunch grass and Yucca glauca. Little is known of the life history of P. m. exiguus, which is restricted to San Martin Island. There is very little rainfall and no permanent water in its habitat (W. H. Burt, verbal communication). Nelson (1921) described the island briefly and stated that the entire surface is covered by extremely ragged and broken lava beds full of numerous pits, caves, jagged points, and sharp ridges. The lava is covered with an abundant growth of lichens. The most notable flowering plants are some cacti and Dudleya anthonyi. P. comanche (Blair, 1943c) was collected in western Texas and probably occupies a restricted range on the rocky cedar-covered slopes along the "break in the plains". This habitat is apparently somewhat less xeric than the Alamogordo region. The area from which this stock was taken is about 300 miles northeast of Alamogordo.

LABORATORY CONDITIONS

The temperature in the combined stock and experimental room was regulated by a commercial type of room thermostat. Humidity was not controlled. Temperature readings were taken several times a day and wet-bulb and dry-bulb thermometer determinations at least once each day.

The mean temperatures for the various experiments ranged from 20.3 to 25.4° C. The lowest temperature recorded during the study was 16.4° C. which occurred only in one experiment. The next lowest temperature recorded was 19.4° C. In the Peromyscus experiments the maximum temperatures ranged from 23.1° to 26.8° C., except in one water-deficiency experiment in which the temperature reached 28.6° C. In an experiment with Perognathus 30° C. was reached. The mean relative humidities for the whole series of experiments ranged from 24 to 47 per cent.

WATER CONSUMPTION BY NONBREEDING ADULT MICE

In order to determine whether the rate of water consumption by the several kinds of small rodents here studied were related to the availability of water in their habitats, the amounts of water drunk by representative individuals of the various races were measured under experimental conditions in which an abundant supply was constantly provided. The amounts of water consumed by more than 500 mice were measured for periods of 10 days or more. In all but 3 determinations (Table II, Series 6, 9, and 11), 10 male and 10 female mice of each of 2 different races were tested concomitantly. The number of mice in the remaining series was limited either by the number of mice or by the cages available at the time. The term "series" is here used to indicate all mice employed at one time in a given experiment; "stock" to designate all mice of a given race collected at a given locality and their descendants.

Methods

The experimental wire-mesh cages, 9 x 15 x 8 inches, occupied a 5-tier rack, the shelves of which had been covered with about 1 inch of wood shavings. Each cage contained cotton, a small nesting chamber, a water bottle, and air-dry food (Dice, 1934). The mice were placed in individual cages in such an order that sexes and races alternated. The positions of the cages on the rack were changed midway in the experiment. At that time the lowest row, near the floor, was exchanged with the top row; the row next to the bottom was exchanged with the row next to the top; the middle row remained in position. The mice were weighed at the beginning, middle, and the end of each experimental period on a beam-type balance calibrated to 0.1 gram. The average of these figures was used as the weight of the mouse.

Distilled water was supplied to each experimental animal by an inverted test tube suspended through a hole in the top of the cage. The open end of the test tube had been heated over a flame until it was reduced to a diameter of about 2.5 mm. A bulge was blown at the closed end to prevent the tube from slipping through the hole. Up and down movements of the tube were prevented by placing a wire cap over the upper end of the tube. The cap was secured to the cage by means of a hinge on one side and a hook on the other. Sidewise movements of the lower tip of the tube, which might jar water from the tube, were prevented by inserting the lower end through an elliptical loop of wire fastened to the side of the cage. Several tests were made in which a mouse was placed in an experimental cage supported over a sheet of paper tinted with washable ink. Any drops of water on the paper left characteristic rings. The watering method was found to operate satisfactorily.

The water tubes were removed from the cage and filled by means of a burette calibrated to 0.1 cc. A fine auxiliary glass tip attached to the bottom of the burette made filling without spilling possible. Twenty additional water tubes were placed in holders on the side of the rack. The amount of water evaporated from these control tubes was measured weekly. At this time the control tubes were exchanged with an equal number of tubes from the experimental cages.

Mice were given at least a day to become accustomed to the new cages. The amount of water required to fill each tube was recorded daily, with few exceptions, for at least 10 days, averaged to a per-day basis, and corrected for evaporation. The time of day at which readings were taken varied somewhat, because day to day comparisons were not planned. The first and last readings of the series, however, were always made at the same time of day. When the tubes were filled they were changed from cage to cage in such a way that any one tube progressed along the rack alternating between races and sexes. Thus, each mouse drank from a different water tube each day, which compensated for any variations in water consumed that may have resulted from small variations in size of the opening in the tubes.

Statistical Treatment

The statistical procedures used in analyzing the data from these experiments follow Snedecor (1946). The coefficient of correlation between the 2 variates measured, body weight and water consumed, was found not to be significant; consequently, treatment was confined to values of the amount of water consumed. Differences which are said to be "highly significant" denote the 1 per cent level of probability; those which are "significant" the 5 per cent level.

Results

A summary, combining the data for males and females, of mean individual weights and of mean daily water consumption for each of the various series of Peromyscus tested is given in Table II, with standard deviations, coefficients of variation of water consumed, coefficients of correlation between body weight and water consumed, and two ratios: (1) water consumed per day per gram of body weight; (2) water consumed per day per square centimeter of body surface as computed from body weight.

Series 1 (Noveboracensis-bairdi). — Noveboracensis drank, on the average, 0.80 cc of water less per day than bairdi. Eight males and 8 females of this series were again tested 3 weeks later for a 12-day period, and in the replication noveboracensis drank an average of 0.86 cc less than bairdi. The difference between species in water consumption is highly significant in both determinations and the difference between trials is not. The same difference was later observed in a test of 8 noveboracensis and 9 bairdi over a 3-day period.

TABLE II

Data on Daily Water Consumption (When Supply is Unlimited) for Males and Females of Several Races of Peromyscus, Including Relation to Body Weight and Body Surface (As Computed from Body Weight)

Sigma = standard deviation, CV = coefficient of variation, r = correlation coefficient.

Series	Race	Number of Mice	Body Weight		Water Consumption			r	Ratio of Daily Water Consumption	
			Mean Individual Weight (gm)	Sigma (gm)	Mean Daily Amount (cc)	Sigma (cc)	CV (Per Cent)		Per Gram of Body Weight	Per cm^2 of Body Surface
1	Noveboracensis†	20	21.09	4.12	2.54	.56	22	.032	.120	.0391
	bairdi	20	18.72	2.88	3.34	.93	28	-.125	.178	.0557
2	Tornillo†	20	31.09	4.79	1.72	.34	20	.536	.055	.0204
	blandus	20	24.50	3.96	2.60	.84	32	.073	.106	.0363
3	Noveboracensis†	20	22.04	5.17	2.46	.44	18	-.325	.112	.0368
	tornillo†	20	27.70	6.29	1.99	.60	30	.294	.072	.0256
4	Bairdi	20	19.71	4.19	3.17	.64	20	.133	.161	.0511
	blandus	20	27.91	4.75	2.96	1.03	35	-.010	.106	.0378
5	Bairdi	20	19.09	4.71	2.37	.59	25	.264	.124	.0390
	nebrascensis	20	21.42	6.22	2.02	.45	22	.159	.094	.0308
6	Bairdi	20	16.75	1.87	3.05	1.02	33	.286	.182	.0548
	rufinus	13	23.72	6.44	2.39	.89	37	-.072	.101	.0341
7	Blandus	20	19.82	2.33	2.38	.74	31	.390	.120	.0382
	eremicus	20	21.09	2.40	2.86	1.05	37	-.229	.136	.0441
8	Eremicus	20	21.42	2.61	1.85	.52	29	.271	.086	.0282
9	Comanche	18	22.61	2.55	3.55	1.13	32	-.110	.157	.0475
	nebrascensis	18	17.89	3.15	1.82	.49	27	-.046	.102	.0313
10	Truei	20	32.40	6.11	2.77	.88	32	-.059	.085	.0321
	exiguus	20	23.78	5.00	3.05	1.06	35	.173	.128	.0435
11	Gracilis stocks									
	Cusino laboratory	10	22.41	1.54	3.21	.48	15	-.133	.143	.0453
	Cusino field	10	17.56	1.86	1.71	.55	32	-.390	.097	.0298
	Norway field	10	24.50	5.63	2.72	.56	21	-.099	.111	.0379

† Field-caught mice.

Series 2 (Tornillo-blandus). — Blandus drank an average of 0.88 cc daily more than tornillo, a difference which is highly significant. This difference between species was also evident in a 3-day series in which 9 blandus and 8 tornillo were tested.

Series 3 (Noveboracensis-tornillo). — Noveboracensis drank 0.47 cc daily more than tornillo, a highly significant difference between races. A 3-day check on 8 mice of each species exhibited this same type of difference.

Series 4 (Bairdi-blandus). — Bairdi consumed 0.21 cc daily more than blandus. Later, when 3 males and 3 females were tested for 4 days, bairdi drank 0.24 cc more than blandus. Neither of these differences between races is significant. In a final test 9 mice of each race were tested for 3 days with no significant difference between races in water consumption.

Series 5 (Bairdi-nebrascensis). — Bairdi drank 0.35 cc per day more than nebrascensis, a significant difference. Later, a series of 9 females each of bairdi, nebrascensis, and tornillo was tested over a 14-day period. Daily water consumption averaged 2.47 cc for bairdi, 1.81 cc for nebrascensis, and 1.60 cc for tornillo. The only highly significant difference was one between species, that between bairdi and tornillo.

Series 6 (Bairdi-rufinus). — Bairdi drank 0.66 cc daily more than rufinus, a difference which is not significant.

Series 7 (Blandus-eremicus). — Blandus drank 0.48 cc per day less than eremicus, a nonsignificant difference.

Series 8 (Eremicus). — A different stock of eremicus, when tested by itself, consumed an average of 1.85 cc of water per day. A daily mean consumption of 1.79 cc was observed in a 6-day trial with 3 females of a third stock of this species.

Series 9 (Comanche-nebrascensis). — Comanche drank 1.73 cc per day more than nebrascensis. This difference is highly significant.

Series 10 (Truei-exiguus). — Truei did not differ significantly from exiguus. The latter species consumed 0.28 cc per day more than the former.

Series 11 (Gracilis stocks). — This test involved 3 stocks of the race P. m. gracilis. The Cusino laboratory stock drank 1.50 cc more than the Cusino field stock, and 0.49 cc more than the Norway field stock. The first difference is highly significant, the second just significant at the 5 per cent level. The Cusino field stock drank 1.01 cc less than the Norway field stock, a highly significant difference.

In addition to the numbered series of Peromyscus, water-consumption data were also obtained for Microtus and Perognathus.

Using the technique described for Peromyscus, a series of 5 males and 6 females of Microtus was tested for a 12-day period and was found to consume an average of 7.23 cc of water daily (from 4.75 to 10.85 cc). In this series the mean of initial and final body weights was 34.70 grams.

The technique for testing Perognathus was identical except that readings of water consumption were made at weekly intervals. A series of 6 males and 4 females of Perognathus were tested over an 8-week period. The average daily consumption of water in this series, after correction for evaporation loss, was 0.038 cc. Four individuals, however, apparently did not use any water at all. Of the two that drank consistently, one averaged 0.19 cc and the other 0.14 cc per day. One individual drank only for a 3-week period, averaging 0.19 cc daily; the remaining 3 were also sporadic, but averaged lesser amounts. Another series of 5 Perognathus of undetermined sex was tested during a 22-day period and found to average 0.20 cc per day (from 0.04 to 0. 51). When tested again over a 13-day period, this series averaged 0.18 cc daily (from 0.03 to 0.38). All of these mice apparently drank some water during each period.

EFFECTS OF DEFICIENT WATER RATION ON BODY WEIGHT AND SURVIVAL

The experiments described above provide information about the amounts of water consumed by several races of rodents when a plentiful supply of water is available. Under this condition water consumption appeared to be highly variable. The question arose, therefore, as to whether the differences between the forms in amounts of water consumed were due to differences in their actual needs or merely to differences in individual preference or habit. In order to ascertain requirements for water in relation to survival, the following studies were made of 8 species and races of mice from habitats of various aridities.

Four of the stocks employed in these experiments originated in the semiarid climate of New Mexico and the other four in the more humid climate of Michigan. The semiarid area was represented by Peromyscus leucopus tornillo, P. maniculatus blandus, P. e. eremicus, and Perognathus penicillatus eremicus; the more humid area by Peromyscus leucopus noveboracensis, P. maniculatus bairdi, P. m. gracilis, and Microtus p. pennsylvanicus.

The effects of deficient water supply were studied by giving the mice progressively smaller daily amounts of water until death occurred. One experiment (Figure 1) compared the weight loss of 2 races of Peromyscus maniculatus, P. m. blandus from the semiarid climate, and P. m. bairdi from the more humid climate, when subjected first to half rations and later to quarter rations of water. A second experiment compared the weight loss and survival time of individuals of 5 races of Peromyscus on reduced water rations (Tables III - V). A third experiment compared weight loss and survival time in 3 stocks of Peromyscus maniculatus gracilis on decreased water rations (Tables VI - VII). Studies were also made of the weight loss and survival time of specimens of Perognathus and Microtus under regimes of deficient water supply (Fig. 1).

Methods

The equipment and techniques employed in the studies of normal water consumption described above were used in the experiments on the effects of a deficient water ration.

Statistical Treatment

The effects of decreased water rations were evaluated by measuring the changes in body weight and by recording observations of survival time. These data were subjected to an analysis of covariance, as described by Snedecor (1946). Differences between adjusted means were tested for significance by Wishart's (1936) modification of the standard test. This modification desensitizes the test in proportion to the degree of difference between means of initial weights.

Because certain animals died during the experiments, plotting the average weights resulted in an erratic line. The use of percentage loss does not smooth the curve. To overcome this difficulty, a weight index has been employed. When a mouse died, the index weight of the remaining mice was obtained by the formula

$$B = \frac{A(W_2' + W_3' + W_4' + \dots\dots\dots W_n')}{(W_2 + W_3 + W_4 + \dots\dots\dots W_n)}$$

where A is the average weight of the mice at the weighing period preceding the death, B is the index weight, W′ is the individual weight at the weighing period following the death, and W is the individual weight prior to the death. Subscripts indicate the individual mice; W_1 would represent the mouse that died.

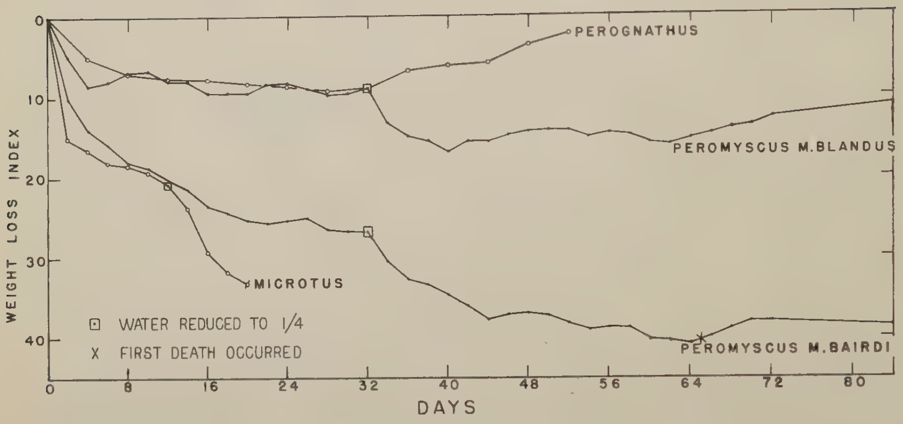


FIG. 1. Weight loss index of Perognathus, on no water, and of two Peromyscus races and of one race of Microtus, both on one-half and on one-quarter water ration.

⊡ Water reduced to one-quarter ration.

x First death occurred.

Results

Experiment 1. The average voluntary water consumption of 3 males and 3 females each of Peromyscus maniculatus blandus and P. m. bairdi was determined, and then each mouse was given, for a period of 32 days, a daily ration equal to one-half its previous average consumption. After this, each individual was placed for 52 days on a further reduced ration, amounting to one-quarter normal consumption. The results, in terms of weight loss index, are presented graphically in Figure 1. In this and subsequent figures, the weight scale represents percentage loss up to the point at which the first death occurred, but thereafter becomes an index of weight lost. This point is marked by a cross on the line for each race. Also indicated are the days on which water was reduced.

The weight-index curves of Figure 1 indicate a similar physiological response on the part of blandus and bairdi to reduced water rations. When placed on half water rations, the mice at first lose weight rapidly, but the weight loss then tends to level off. Reduction of the ration to one-quarter normal results in further loss followed by slight gains. It is likely that some gain would also have been recorded on half rations had the mice been continued long enough on that regime. After 4 days on half rations, blandus showed a stabilization of weight with only moderate daily fluctuations thereafter; the final weight of blandus after 32 days on half rations was only slightly lower than that attained after 4 days. Bairdi lost weight over a longer period, at first more rapidly than blandus, then at a slower rate, and finally leveled off after a weight loss greater than that suffered by blandus.

In this first experiment (Fig. 1), the normal daily water ration was 2.66 cc for bairdi and 2.46 cc for blandus. When first placed on half ration, the average body weight for bairdi was 23.00 grams and for blandus was 21.58 grams. After 32 days on half ration, the mean weight for bairdi was 16.88 grams and that for blandus was 19.70 grams, indicating a weight loss of 27 per cent for the former and 9 per cent for the latter. Following the shift to quarter ration further loss in weight occurred, amounting on the average to 3.08 grams for bairdi and 1.90 grams for blandus. The difference between initial and final weights represents a loss of 37 per cent for bairdi and 10 per cent for blandus.

At the half water ration, the partial correlation between the amount of water consumed and the weight lost independent of initial weight was +.028 and that between water consumed and initial weight independent of weight lost was + .074. Neither of these values is a significant one. Evidently no particular advantage is gained by giving each mouse a specified fraction of its voluntary water consumption. In subsequent experiments, therefore, a uniform subminimal ration was given to each individual.

The variability in initial weights among individuals of both races is not markedly different from that in final weights. The coefficient of variation of initial weights was 17 per cent for bairdi and 21 per cent for blandus; that of final weights was 13 per cent for bairdi and 14 per cent for blandus. The partial correlation between initial weight and final weight, independent of water consumed, was +.967, a highly significant value. The final weight of an individual mouse is is evidently conditioned by its beginning weight. It is apparent, therefore, that the actual difference, 2.82 grams, between the mean weights of bairdi and blandus, after 32 days on half ration, does not give a very accurate measure of racial difference. The effect of initial weight can be controlled by use of the regression equation, whereby the final weights are adjusted to a uniform initial weight, and the differences between adjusted final weights can be tested for significance. The individual race regressions were not significantly different from the mean regression of both races and, consequently, the average regression was used in obtaining the adjusted means.

With an initial adjusted weight of 22.29 grams, the adjusted mean weight after 32 days on half water ration was 16.57 grams for bairdi and 20.01 grams for blandus. The difference of 3.44 grams between the 2 races is highly significant. The adjusted mean weight after 32 days on quarter ration was 13.14 grams for bairdi and 18.74 grams for blandus, giving an adjusted total weight loss of 9.15 grams for bairdi and 3.55 grams for blandus. The difference in total weight loss is highly significant.

Experiment 2. Five races of Peromyscus were placed on reduced water rations. Three males and 3 females each of Peromyscus leucopus noveboracensis, P. l. tornillo, P. maniculatus bairdi, P. m. blandus, and P. e. eremicus received a deficient supply of water for an extended period during which they were weighed at 2-day intervals. The groups, in the order named, while started at different times, were run concomitantly throughout most of the experiment. No abnormal fluctuations in the laboratory environment were noted during the 3 weeks in which the various groups were started; hence, it is believed that the lack of a common date of origin did not introduce any appreciable error into the experiment.

The average daily normal consumption of water for the mice used in this experiment was as follows: noveboracensis, 2.4 cc; tornillo, 2.0 cc; bairdi, 3.8 cc; blandus, 3.2 cc; and eremicus, 1.8 cc. In order to avoid a large initial reduction for the races of leucopus and maniculatus, which normally drink more water than eremicus, these forms were placed on half rations for several days. Later, the water ration was reduced to 0.9 cc, followed by reduction to 0.4 cc, then to 0.2 cc, and finally to no water at all.

The mean-weight index obtained in this experiment, together with the times at which the reductions in water ration were made, are shown graphically in Figure 2. It is apparent that the general trends duplicate those of the preceding experiment. The weight-loss curve drops rapidly at first and then levels off. Evidence of this trend is noted at each water-ration level for all races except noveboracensis, which was unable to adjust to the 0.2 cc ration. The races differ in their ability to adjust to reduced amounts of water, as indicated by differences in mean final weights on each water ration, by the curvature of the weight-index lines, and by the differences in weight gain after the initial loss.

Correlations between initial weight and final weight on each water ration are as follows: +.758 on half ration; +.814 on 0.9 cc; +.653 on 0.4 cc; and +.654 on 0.2 cc. These values are all highly significant. It was necessary, therefore, to make adjustments for differences in initial weights, as in the previous experiment. The mean final weights, adjusted to a mean initial weight of 23.77 grams, at each water ration are given in Table III and the differences between the adjusted means for the 0.9 cc ration are listed in Table IV.

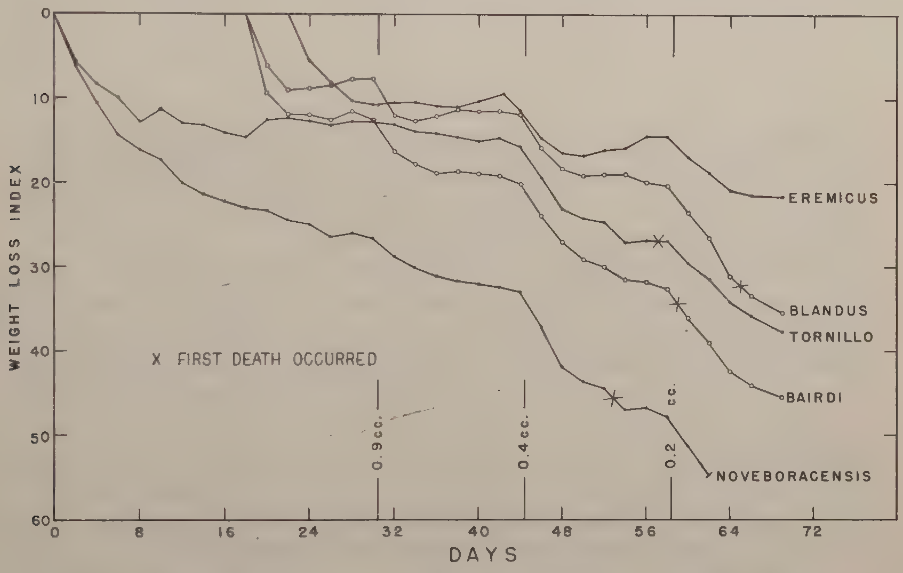


FIG. 2. Weight loss index of five races of Peromyscus on reduced water rations.

One-half ration for eremicus amounted to 0.9 cc and no change was made until all races received 0.4 cc water ration.

x First death occurred.

On half water ration the differences in adjusted mean final weights between noveboracensis and the other races were highly significant. In each comparison noveboracensis weighed less. Differences between the remaining races were not significant.

At the end of the 0.9 cc daily water-ration period, noveboracensis also weighed significantly less than the other races. Bairdi weighed significantly less than blandus or eremicus, but the differences in body weight between the other races were not significant.

TABLE III

Mean Final Individual Weights For Five Races of Peromyscus
Adjusted to a Mean Initial Weight of 23.77 Grams

Race	Mean Final Weight (in gm) on Daily Water Ration of			
	One-half	0.9 cc	0.4 cc	0.2 cc
Bairdi	20.15	18.51	15.70	13.62
Blandus	22.12	21.10	19.05	16.58
Noveboracensis . .	17.56	15.96	12.58	. . . .
Tornillo	21.16	20.40	18.32	15.92
Eremicus	20.82	20.80	20.04	18.33

Differences on 0.4 cc of water daily diverged from differences at 0.9 cc in only 2 respects. The bairdi-blandus difference was significant at the 2 per cent level and the bairdi-eremicus difference was significant at the 1 per cent level.

Differences between adjusted mean final weights on 0.2 cc water daily were not significant. By this time more than one-third of the mice had died, and the reliability of the test is questionable. Nevertheless, as shown in Figure 2, subjection to this low water ration

TABLE IV

Differences in Adjusted Mean Final Weights of the Five Races
of Peromyscus on a Daily Water Ration of 0.9 cc

Race	Difference (in gm) in Adjusted Mean Final Weight			
	Bairdi	Blandus	Noveboracensis	Tornillo
Blandus	+2.59*	. . . .	. . . .	. . . .
Noveboracensis . .	-2.55*	-5.14**	. . . .	. . . .
Tornillo	+1.89	-0.70	+4.44**	. . . .
Eremicus	+2.29*	-0.30	+4.84**	0.40

*Significant (5 per cent level).

**Highly significant (1 per cent level).

Plus or minus signs indicate whether the difference between the races is more or less than the one with which it is compared; that is, blandus weighed 2.59 grams more than bairdi; noveboracensis, 2.55 grams less.

accentuated the differences between races in all instances except that of the blandus-tornillo comparison.

The variability in final weights on 0.2 cc of water was similar to that in weights at the beginning of the experiment. The coefficient of variation of initial weights for the different races ranged from 6 to 26 per cent, and that of final weights from 14 to 24 per cent. On the basis of adjusted mean final weights on the 0.2 cc ration, eremicus lost 23 per cent of its weight in the course of the experiment, blandus lost 30 per cent, tornillo lost 33 per cent, and bairdi lost 43 per cent. The 3 noveboracensis which survived for only 3 days on this ration lost an average of 53 per cent of their initial weight.

TABLE V

Means of Initial Weight, Weight Loss, and Survival Days (with the Extremes) of Individuals of Five Races of Peromyscus on Various Water Rations

Race	Mean Initial Weight (in gm)	Mean Weight Loss (in gm) on Daily Water Ration of			Survival Data		
		0.9 cc	0.4 cc	0.2 cc	Mean of Days Lived	Days to First Death	Days to Last Death
Noveboracensis	25.27	8.35	12.07	. . .	17	9	19
Bairdi	20.97	4.21	6.87	9.17	24	17	30
Tornillo	25.60	4.03	6.66	9.72	28	13	39
Blandus	24.32	2.87	4.95	7.30	29	21	42
Eremicus	22.68	2.58	3.26	4.91	41	34	44#

# Three mice still alive.

Probably the best criterion for evaluating the effect of reduced water ration is the length of time a mouse can survive on it. Average initial weights, weight losses, and survival days of these 5 races of Peromyscus are given in Table V. Because the mice were started in the experiment at different times, total survival days cannot be used as a basis of comparison. However, the period on 0.4 cc of water daily and the subsequent period on 0.2 cc were of equal duration for all races. Since all of the mice apparently reached a stable weight on 0.9 cc daily of water, it is believed to be a proper reference point from which survival time can be counted.

Eremicus survived an average of 41 days after the water ration was reduced to 0.4 cc daily. This was the longest survival time and the differences between it and all other races are highly significant. Three eremicus died, before the experiment was closed, after 44 days on this ration, and the 3 remaining mice were given water thereafter. Forty-four days is, therefore, used as the survival time for these individuals in computing the mean for this race.

Noveboracensis was least well able to survive and lived an average of 17 days after the daily ration of water was reduced to 0.4 cc. The differences between it and the other races are highly significant, except for the comparison with bairdi, which is significant at the 5 per cent level.

Bairdi survived an average of 24 days on 0.4 cc water ration, tornillo 28 days, and blandus 29 days. Differences in survival time between these races are not significant.

Series of both Microtus pennsylvanicus and Perognathus penicillatus were also tested on a deficient water supply in this second experiment. Six male Microtus were placed in separate cages and each was given 3.4 cc of water daily, one-half their average normal consumption, for a period of 12 days. This was followed by a further reduction to 1.8 cc daily for an additional 10 days. Throughout both periods the mice were weighed at 2-day intervals. The results are shown graphically in Figure 1.

The weight-loss curve, though not complete, indicates a trend like that of Peromyscus, particularly bairdi, but at a slightly lower level. On half water ration, most of the loss occurs during the first 4 days, and the weight loss tends to level off thereafter. Following this initial loss, some weight gain was observed; 3 individuals gained an average of 0.61 grams from their lowest weights. On 1.8 cc of water daily the curve was similar except that no gains in weight followed the initial loss. In this experiment the mean survival time for Microtus was 18 days, with the first death occurring after 9 days and the last after 22 days. The 3 individuals which survived the experiment died within 2 days after all water was removed.

Three males and 3 females of Perognathus were confined in separate cages and fed the same type of food used for Peromyscus bue given no water. These mice were weighed every 4 days. Figure 1 also indicates the trend of weight loss and gain in this series. The mean weight of the Perognathus decreased for 28 days, most rapidly during the first 8 days, and then gains in weight were made for 24 days. One male gained throughout the experiment, and the mean final weight of the others was only 3.6 per cent below their initial mean weight. Perognathus was able to survive at least 52 days without water, and 2 individuals were kept on this regime for 81 days each without any apparent harmful effects.

Experiment 3. Three stocks of Peromyscus maniculatus gracilis were tested on deficient water rations. The decrease from normal consumption to 0.9 cc daily was made in one step, followed by further reductions to 0.4 and 0.2 cc, respectively. The 0.9 and 0.4 cc ration were maintained for 22 days each, and the 0.2 cc period lasted 32 days. All except one mouse died on the 0.2 cc ration, and this individual received water when it appeared likely to succumb if the experiment were continued. Weights were taken daily during the first week and every 2 days thereafter, except for the last few weighings, which were made at 3-day intervals. Weight trends are shown graphically in Figure 3.

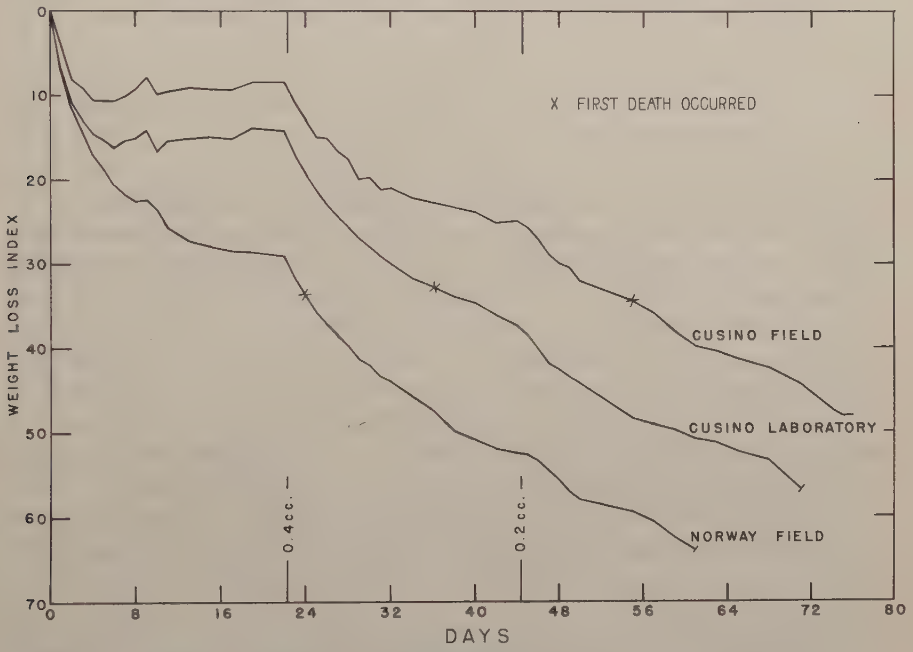


FIG. 3. Weight loss index of three stocks of Peromyscus m. gracilis on reduced water rations of specified daily amounts.

x First death occurred.

Weight changes were very much like those of the preceding experiments. The single-step reduction of water to a 0.9 cc ration increased somewhat the rate of weight loss but was not seriously detrimental to the mice. Both the Cusino field-caught stock and the Cusino laboratory-bred stock were able to stabilize their weights at a lower level, and the curve of Figure 3 suggests that the Norway field-caught stock might have done so had it been given more time. On the 0.4 cc ration, the tendency to stabilize weight was evident only in the Cusino field stock, and it was not appreciably

TABLE VI

Mean Final Weights of Three Stocks of Peromyscus m. gracilis
Adjusted to an Initial Mean Weight of 23.77 Grams, with Differences and Significance
at the 0.9 cc Water-ration Level

Stock	Mean Final Weight (in gm) on Daily Water Ration of		Weight Difference (in gm) on 0.9 cc Daily Water Ration	
	0.9 cc	0.4 cc	Cusino Laboratory	Norway Field
Cusino laboratory. .	18.32	13.92		
Norway field	15.54	13.93#	2.78**	. . . .
Cusino field	17.79	14.14	0.53	2.25**

**Highly significant (1 per cent level).
#Only two mice were alive.

noticeable on the 0.2 ration. When placed on this lowest ration, loss in weight took place at an almost uniform rate until death occurred. None of the individuals was able to gain weight after initial losses.

The coefficient of variation in initial weights ranged from 7 to 21 per cent, that in final weights on 0.9 cc daily from 11 to 14 per cent, and that in final weights on 0.4 cc daily from 8 to 11 per cent. The mean final weights on the 0.9 cc ration, adjusted to a mean initial weight of 23.77 grams (identical with that used in Experiment 2), and the differences between them are shown in Table VI.

The correlation +.709 between initial and final weights on 0.9 cc of water daily is highly significant. At the end of this period, both

TABLE VII

Means of Initial Weight, Weight Loss, and Survival Days (with the Extremes)
of Individuals of Three Stocks of Peromyscus m. gracilis on Various Water Rations

Stock	Mean Initial Weight (in gm)	Mean Weight Loss (in gm) on Daily Water Ration of			Survival Data		
		0.9 cc	0.4 cc	0.2 cc	Mean of Days Lived	Days to First Death	Days to Last Death
Cusino laboratory. . .	21.66	3.06	7.61	. . . .	49	35	71
Cusino field	18.04	1.51	4.49	. . . .	64	50	75#
Norway field	23.31	6.79	7.75	. . . .	39	24	62

#One mouse was still alive.

of the Cusino stocks were significantly heavier than the Norway stock, but the difference between the Cusino field and the Cusino laboratory stocks was not significant. The adjusted final weights on the 0.4 cc water ration are not significantly different.

Table VII presents the data on initial weights, weight losses, and survival times of these 3 gracilis stocks. Unfortunately, no reference point is available for comparison with the 5 Peromyscus races tested in Experiment 2. The mean weight loss of the Norway field stock on the 0.4 cc ration is based on the records of the 2 individuals which survived this period; since these were from the top of this stock's weight range, the value of 7.75 is somewhat low. The mean survival time of the Cusino field stock includes a figure of 75 days for one individual that was given water after that time. On these reduced water rations, the Cusino field stock survived 15 days longer than the laboratory stock from the same area and 25 days longer than the Norway field stock from about 65 miles away. These differences are highly significant. The difference in survival time between the Cusino laboratory stock and the Norway field stock is significant at the 5 per cent level. None of these gracilis stocks was able to survive on 0.2 cc of water daily, in this resembling noveboracensis. From an inspection of Table VII it appears that the mice which lose weight most slowly survive the longer.

DIFFERENCES IN WATER REQUIREMENTS OF MICE FROM HUMID AND FROM XERIC HABITATS

Although it has long been known that the water requirements of certain animals have a definite relation to survival, especially in xeric habitats, few critical studies of the water requirements of the smaller mammals have previously been made. In a study of the food and water requirements at various temperatures and humidities of Microtus ochrogaster, Peromyscus leucopus, and P. maniculatus, Dice (1922) failed to find differences between the water needs of the 2 Peromyscus species sufficient to be the basis of habitat preference within the same climatic area. Ross (1930) studied the comparative water intake of 5 races of laboratory-bred Peromyscus belonging to the species maniculatus and eremicus. When comparisons were made on the basis of water consumed per gram of body weight, significant differences were reported between species but not between races of the same species. Ross concluded that the races P. m. gambeli, P. m. rubidus, P. m. sonoriensis,

P. e. eremicus, and P. e. fraterculus had not diverged sufficiently in their evolutionary development to display differences that could be detected with the techniques he used.

Of fundamental importance in the study of water requirements of animals from different habitats is the basis of comparison. Shall the water consumed by the different animals be compared in terms of water consumption per individual, or in terms of water consumption per gram of body weight, or in terms of water consumption per unit surface area? In a study of water intake in the rat Richter and Brailey (1929) used as their measure of comparison the water consumed per unit of body surface area. Surface area is generally not measured directly, but is calculated from a formula in which the surface area is equal to a constant times the two-thirds power of the weight. In the present study several trial computations of surface area were made, using (a) the constant 8.5 for Peromyscus as reported by Pearson (1947) and (b) the constant of 9.1 used by Richter and Brailey (1929) for the rat. In no instance was the computed surface area found to be significantly correlated with the quantity of water consumed.

Water consumed per gram of body weight was employed in the studies of Dice (1922) and Ross (1930). The ratio of water consumed per gram of body weight was not employed as a basis of comparison in the present study, because in the analysis of covariance the regressions that were used involved weight and water as the variates. Correlations between body weight and water consumed were computed for each of the series of paired observations shown in Table II, for the races within each series, and for the sexes of each race. None of the correlations was significant at the 1 per cent level, and the number significant at the 5 per cent level did not deviate greatly from the expected occurrence of one in 20 trials. Replications showed considerable inconsistency. It was therefore assumed that in these instances body weight and water consumed were not correlated to any marked degree. This is apparently not true, however, of young individuals which are actively growing. Lindeborg (1950) found that water consumption increases with weight in growing young of Peromyscus maniculatus bairdi; Richter and Brailey (1929) discovered a similar trend in growing white rats.

Sex differences likewise had no discernible effect upon water consumption. Each of the series of observations recorded in Table II extended over at least 1 and in many cases over 2 estrous periods (Clark, 1936), and any differences in water consumption between males and females due to modified physiology during these periods should have been reflected in the data. For the 22 male : female comparisons available, only twice were the differences significant.

Since these differences might have been due to random sampling, it was concluded that males and nonbreeding females did not differ in amounts of water consumed.

Dice (1922) and Ross (1930) also considered the amount of water consumed per individual. In the present study the amounts of water consumed by individual mice in successive determinations about a month apart were measured for 3 races of Peromyscus. There were no significant differences between the determinations of the various individuals. Evidently the average amounts of water consumed by an individual under constant conditions remains quite consistent. Differences in the mean consumption per individual are thought to be a satisfactory basis for making comparisons.

The most striking differences in daily water consumption were those between genera of mice inhabiting different geographic areas. As already noted, the Michigan specimens of Microtus averaged 7.23 cc of water daily, in contrast to the mean of 0.038 cc consumed per day be those of Perognathus from New Mexico. The several species and races of Peromyscus were all intermediate between these two, so far as consumption of water is concerned.

The amounts of water consumed by the various species of Peromyscus from different habitats within the same climatic region were not conclusively different. A comparison of races from different geographic areas yielded highly significant differences between noveboracensis from Michigan and tornillo from New Mexico (at the 1 per cent level) and a significant difference between bairdi from Michigan and nebrascensis from the Sand Hills of Nebraska, but there were no significant differences between Michigan bairdi and either blandus or rufinus from New Mexico, or between truei from New Mexico and exiguus from San Martin Island. Mice originating in areas with more mesophytic vegetation apparently drink more water than those from primarily xerophytic regions. In seeming exception to this statement, comanche from western Texas drank more than nebrascensis, but it is quite possible that the amount of water actually available to these mice in their respective habitats may not be accurately reflected by known data.

Significant differences were also found between 2 stocks of the same race originating in the same climatic area. The Norway stock of gracilis from Michigan consumed significantly more water daily than the Cusino stock.

The differences noted above are all differences in voluntary water consumption. Voluntary consumption of water varied a great deal between individuals of all the races studied, and there was considerable overlap of measurements in each series. Conclusions based solely on differences in the amounts of water consumed voluntarily by various races of Peromyscus are not very reliable for the estimate of water needs in nature. Nevertheless, these experiments do show that, however inadequate voluntary water consumption may be as a basis of comparison, it definitely supports results obtained from the study of other aspects of water metabolism.

One of the other aspects of water metabolism studied was the response to a deficient supply of water. When the water ration of the various races was decreased to one half that voluntarily consumed, the mice lost weight, rapidly at first and more slowly later, until a weight level was reached beyond which no further loss occurred. If sufficient time is allowed on a reduced ration, the mouse may regain some or all of the weight lost. This suggests that the mouse becomes physiologically adjusted to the water deficiency. If further reductions in water ration are made, a similar response is usually evident. Reduction may reach a point, however, at which the mice are no longer able to adjust their physiological requirements to the amount of water received, in which case they lose weight steadily and soon die. The rate at which weight is lost apparently depends upon the amount of water provided and upon the species and race of mouse. The weight level maintained on any given water ration and the total survival time depend on these same factors and also on the length of time the mice have been held on the various rations.

The ability to regain eventually some of the initial weight lost after a reduction in water ration is apparently possessed by some races and not by others. This subsequent gain of weight is important in that it emphasizes the physiological nature of the adjustment to water deficiency. Evidently some forms are able to utilize water or to reduce their rate of water loss more efficiently than others. In a study of the water exchanges of some small mammals, Chew (1951) reported that in Peromyscus, when water drinking was restricted, most of the water conservation which occurred was effected by a reduction in urine volume. Racial differences in ability to adjust to water deficiency when the water was reduced to the same amount for all mice were similar to those observed when the reduction was proportional to the voluntary consumption. It is concluded, therefore, that the ability to maintain weight on a deficiency of water is a characteristic of race.

The most striking differences in adaptation to conditions of varying water deficiency were those between genera. Of all the forms tested, individuals of Perognathus lost the least weight, even though no water at all was provided them. All of these pocket mice in each experiment with deficient water rations survived the entire experimental period. Lindeborg (MS) has subsequently found that Perognathus is able to prevent loss of water through skin and lungs; in completely dry air it lost an average of only 0.80 cc of water per day, whereas Peromyscus leucopus tornillo lost 2.33 cc daily and P. l. noveboracensis slightly more. Perognathus is apparently better adapted for life in an arid habitat than any of the other forms studied.

Microtus showed the least ability to survive on a deficient water supply. Three of 6 individuals failed to survive on 1.8 cc of water daily, while all Peromyscus survived on lesser amounts. When placed on half ration 1 Microtus died, and 2 individuals succumbed on quarter ration. Although none of the races of Peromyscus was able to survive without water, all survived on half ration and only one died on quarter ration. Peromyscus seems to occupy a position intermediate between Perognathus and Microtus in its ability to survive a deficient water supply.

The differences in adjustment to water deficiency exhibited by various races of a given species, though less marked than those between genera, were nonetheless clear. Peromyscus leucopus tornillo not only survived longer on reduced rations than P. l. noveboracensis, but was also able to maintain a higher weight level on all water rations. Likewise, Peromyscus maniculatus blandus survived longer on no water than P. m. bairdi and maintained a higher weight level at each water ration. Within each of the species maniculatus and leucopus, the races which inhabit the more arid regions proved to be somewhat better able to live with reduced water rations than those which inhabit more humid regions.

The correlation between ability to survive on a reduced water supply and occurrence in arid or more humid conditions is also evident in a comparison of forms occupying different habitats in the same geographic region. P. m. bairdi survived longer and maintained a higher weight level than P. l. noveboracensis; in southern Michigan, bairdi lives in grassland which is drier than the woodland habitats occupied by noveboracensis. Likewise, P. eremicus maintained higher weight levels and survived longer than either P. l. tornillo or P. m. blandus; in New Mexico, eremicus lives mainly in rocky situations, blandus in mesquite areas, and tornillo in grassy washes. Eremicus is evidently better adapted to life under conditions of water deficiency than are any other of the forms of Peromyscus tested.

Changes in weather and season must cause considerable variation in the amounts of water available in the habitats of all the mice studied. It has already been shown (Kincer, 1922) that periods of 70 days with less than 0.25 of an inch of rain may occur in southern New Mexico. Perognathus survived for 81 days on air-dry food and no water and would experience little difficulty because of drought conditions. The various Peromyscus races tested could survive extended dry periods. One-half of these mice survived 55 days and some of each race lived at least 66 days on reduced water rations. Periods of 49 days with 0.25 of an inch of rain or less may occur in southern Michigan. One-half of each Peromyscus race tested from this region lived 47 days on reduced water rations and, therefore, could certainly survive extensive seasonal periods of drought. Microtus, however, lived only 22 days on reduced water ration and would find extended dry periods critical to survival.

Lindeborg (1950) has suggested that breeding can take place only when the supply of moisture in the habitat is ample. During the breeding season, nursing bairdi females require more than twice as much water as nonbreeding females. There is a midsummer lull in the breeding activities of this race when temperatures are high and moisture low. It is also possible that subjection to water deficiency while young may be detrimental to future breeding.

In the evolution of races and of species adapted to xeric habitats, mutation and selection of physiologic characters must have played as important a role as that of such morphological characters as dentition, body dimensions, and pelage color. Adjustment of the breeding season to coincide with periods when sufficient water is available to bring the young through to weaning age is an especially important adaptation that presumably is also subject to selection. During its evolution Perognathus p. eremicus evidently developed special physiological adaptations to water deficiency which fit it almost perfectly for life in extremely dry habitats. Microtus p. pennsylvanicus, on the other hand, has not acquired these physiological adaptations to any appreciable degree and is therefore confined to the more mesic habitats. Of the various species of Peromyscus tested eremicus is best adapted to xeric habitats and maniculatus seems to have progressed further in this direction than leucopus.

SUMMARY

When an abundance of water was supplied under controlled laboratory conditions to adult nonbreeding mice, individual voluntary consumption ranged from no water at all by some pocket mice, Perognathus penicillatus eremicus, to 10.85 cc daily by some voles, Microtus p. pennsylvanicus. The average voluntary consumption by series of individuals was least in Perognathus, greatest in Microtus, and intermediate in the several species and races of Peromyscus tested. Differences in voluntary consumption were greatest between genera, but were also observed between species of the same genus and between races of a given species. A significant difference in water consumption was demonstrated between two stocks of Peromyscus maniculatus gracilis captured in similar habitats about sixty-five miles apart.

When given a water ration less than that consumed voluntarily, all of the forms tested lost weight. Under a reduced water ration, weight is lost rapidly at first, then at a decelerating rate, until a weight level is reached beyond which no further loss occurs. If this regime is continued long enough, individuals of some races may regain weight. All of the forms tested were able to survive on reduced water rations. If the reduction is too severe, however, a mouse may be unable to adjust its physiological requirements to the amount of water received, and it will lose weight steadily until death ensues. The rate of weight loss is dependent on the amount of water provided and on the species and race. Differences in the ability to survive a reduced water ration were also greatest between genera. Individuals of the genus Microtus survived least well on a deficient water ration, whereas those of Perognathus were able to survive on no water at all. The various races of the species of Peromyscus studied likewise differed in their ability to withstand water deficiency.

Within each species of Peromyscus tested the races which consumed least water, when an abundance was provided, and which were best able to survive a reduced water ration were those that naturally live in the more xeric climatic areas. In each climatic area studied, the forms which were better able to survive on deficient water lived in the more xeric habitats. Peromyscus eremicus lived longer and maintained a higher weight level on reduced water rations than any of the other deermice tested; the desert habitats in which this species lives are very arid.

In the evolution of races and species adapted to xeric habitats, selection for the ability to survive a deficient water supply is believed to have played an important role. It is also reflected in the adjustment of breeding season to coincide with periods when sufficient water is available to bring the young through to weaning age. Such physiological characters are as distinctive of taxonomic species and races as are morphological characters.

LITERATURE CITED

BENEDICT, F. G.

1938 Vital energetics. A study of comparative basal metabolism. Carnegie Instit. Wash. Publ., 503. 215 pp.

BLAIR, W. F.

1940 A study of prairie deer-mouse populations in southern Michigan. Amer. Midl. Nat., 24: 273-305.

1941 Annotated list of mammals of the Tularosa Basin, New Mexico. Journ. Wildlife Management, 26: 218-29.

1943a Ecological distribution of mammals in the Tularosa Basin, New Mexico. Contrib. Lab. Vert. Gen. Univ. Mich., 17: 1-10.

1943b Populations of the deer-mouse and associated small mammals in the mesquite association of southern New Mexico. Contrib. Lab. Vert. Biol. Univ. Mich., 21: 1-40.

1943c Biological and morphological distinctness of a previously undescribed species of the Peromyscus truei group from Texas. Ibid., 24: 1-8.

BURT, W. H.

1940 Territorial behavior and populations of some small mammals in southern Michigan. Misc. Publ., Mus. Zool. Univ. Mich., 45: 1-58.

CHEW, R. M.

1951 The water exchanges of some small mammals. Ecol. Monogr., 21: 215-25.

CLARK, F. H.

1936 The estrous cycle of the deer-mouse, Peromyscus maniculatus. Contrib. Lab. Vert. Gen. Univ. Mich., 1: 1-7.

DICE, L. R.

1922 Some factors affecting the distribution of the prairie vole, forest deer-mouse, and prairie deer-mouse. Ecology, 3: 29-47.

1929 A new laboratory cage for small mammals, with notes of methods of rearing Peromyscus. Journ. Mammalogy, 10: 116-24.

1930 Mammal distribution in the Alamogordo region, New Mexico. Occ. Papers Mus. Zool. Univ. Mich., 213: 1-32.

1934 An improved Peromyscus ration. Journ. Mammalogy, 15: 160-61.

1940 The Tularosa Malpais. Sci. Mon., 50: 419-24.

1942 Ecological distribution of Peromyscus and Neotoma in parts of southern New Mexico. Ecology, 23: 199-208.

HALL, F. G.

1922 The vital limit of exsiccation of certain animals. Biol. Bull., 42: 31-51.

HARRIS, J. A., and F. G. BENEDICT

1919 A biometric study of basal metabolism in man. Chapter VI. A critique of the body-surface law. Carnegie Instit. Wash. Publ., 279. 266 pp.

KINCER, J. B.

1922 Atlas of American agriculture. Part II, climate. Section A, precipitation and humidity. U. S. Dept. Agric., Office Farm Management, Advance Sheet 5 (March 15): 1-48.

LINDEBORG, R. G.

1948 Water requirements of certain rodents from xeric and mesic habitats. Ann Arbor, Mich.: University Microfilms. (Microfilm).

1950 An adaptation of breeding Peromyscus maniculatus bairdii females to available water, and observations on changes in body weight. Journ. Mammalogy, 31: 74-78.

MS Water conservation in Perognathus and Peromyscus.

MILLER, G. S.

1923 List of North American recent mammals. Bull. U. S. Nat. Hist. Mus., 128: 1-673.

NELSON, E. W.

1921 Lower California and its natural resources. Mem. Nat. Acad. Sci., 16: 1-194.

NELSON, E. W., and E. A. GOLDMAN

1932 The name of the San Martin Island Mouse, a correction. Journ. Mammalogy, 13: 370-71.

PEARSON, O. P.

1947 The rate of metabolism of some small mammals. Ecology, 28: 127-45.

POOL, R. J.

1912 Glimpses of the great American desert. Pop. Sci. Mon., 80: 209-35.

RICHTER, C. P., and M. E. BRAILEY

1929 Water-intake and its relation to the surface area of the body. Proc. U. S. Nat. Acad. Sci., 15: 570-79.

ROSS, L. G.

1930 A comparative study of daily water-intake among certain taxonomic and geographic groups within the genus Peromyscus. Biol. Bull., 59: 326-38.

SNEDECOR, G. W.

1946 Statistical methods applied to experiments in agriculture and biology. 4th ed.; Ames, Ia: Iowa State College Press.

WISHART, J.

1936 Tests of significance in covariance. Journ. Roy. Statist. Soc., Suppl. 3: 79-82

Biology Department, New Mexico Highlands University, Las Vegas, New Mexico

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price $0.45.

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

University of Michigan, Ann Arbor, Michigan

Number 59 February, 1953

THE MEASUREMENT OF FERTILITY AND ITS USE AS AN INDEX OF REPRODUCTIVE ISOLATION AMONG CERTAIN LABORATORY STOCKS OF PEROMYSCUS

By T. T. LIU

Accepted for publication September 15, 1952

CONTENTS

Introduction 1
Materials and Methods 2
Analysis of Data 6
Summary 11
Literature Cited 12

INTRODUCTION

MOST previous studies of hybridization have been restricted to its qualitative aspects. Quantitative measurements of the fertility relationships within and between species are urgently needed. To meet this need some simple formulae are here presented which have been derived in an attempt to evaluate the fertility of parent stocks as well as the amount of reproductive isolation which is involved in intersubspecific and interspecific crosses in Peromyscus.

Mice of the genus Peromyscus offer a unique opportunity for the study of hybridization. They occupy a variety of ecologic niches and are divided into many species and subspecies. Most species can be bred in the laboratory, and some interspecific and intersubspecific crosses are successful (Dice, 1933).

Acknowledgments

I wish to express my sincere appreciation to Dr. J. V. Neel for his valuable advice and guidance during the progress of this study. I also

wish to thank Dr. L. R. Dice and Dr. F. C. Evans for their suggestions and criticisms in the preparation of this paper and Dr. W. J. Schull, Dr. F. E. Smith, and Mr. W. B. McIntosh for their valuable advice on statistical methods. Mr. P. J. Clark carefully read the manuscript and made many helpful suggestions. The study was conducted in the Laboratory of Vertebrate Biology.

MATERIALS AND METHODS

The stocks of mice used are as follows:

Peromyscus maniculatus blandus.— Taken in the vicinity of Tularosa, Otero County, New Mexico, in 1938, by W. F. and F. A. Blair.

P. maniculatus bairdi. — Taken in Washtenaw County, Michigan, in 1946.

P. polionotus leucocephalus. — Taken on Santa Rosa Island, Florida, in 1942, by W. F. Blair.

The animals were reared by the general methods described by Dice (1947). Only individuals from about two months to one year of age were used in the matings. Close inbreeding was avoided, and all matings in which the relationship was closer than first cousin were excluded. Each mating was examined for litters every day for a period of six months, starting three weeks after the mating was made. Those matings which produced one or more live-born young were considered to be fertile. The sterility of some mated females was later confirmed by the absence of placental scars in their uteri.

Formulae for the Measurement of Fertility and of Reproductive Isolation

Before an attempt is made to analyze or to interpret the experimental results, certain formulae needed for the measurement of fertility and of reproductive isolation are presented and, when necessary, a brief explanation is given of their derivation.

Only a fraction of laboratory-bred animals is fertile, as is probably true of field-living animals. This is undoubtedly due to many factors, involving both heredity and environment. It is first necessary, therefore, to make an estimate of the probability of an individual's being fertile. If b is the number of fertile matings among the total number, n_1, of matings made, and if it is assumed that f, the probability of fertility, is equal and independent in the two sexes (this point will be discussed later), then the proportion of fertile matings is equal to the probability of a fertile female being mated with a fertile male, or $b/n_1 = f^2$. From this relationship the probability of an individual mouse being fertile is readily obtained as $f = \sqrt{b/n_1}$.

Therefore, the following relations are obtained:

Proportion of fertile matings,

$$f^2 = \frac{b}{n_1} \qquad (1)$$

Probability of an individual being fertile,

$$f = \sqrt{\frac{b}{n_1}}. \tag{2}$$

The standard deviation (S) of f is easily obtained by the maximum likelihood method (Mather, 1951), as follows:

$$S_f = \sqrt{\frac{1 - f^2}{4n_1}}. \tag{3}$$

Since it is not infrequent that certain males have been previously proved to be fertile, the probability of these males being fertile is unity, and as a result the proportion of fertile matings, c, among total matings, n_2, involving these males should be equal to the proportion of fertile females among the total number of females used. That is:

Probability of an individual female being fertile,

$$f = \frac{c}{n_2}. \tag{4}$$

The standard deviation in this case is:

$$S_f = \sqrt{\frac{f(1-f)}{n_2}}. \tag{5}$$

Consequently, two different f values, f_1 and f_2, may be calculated from the separate sets of data obtained from different mating types, that is, f_1 is calculated from one set of data gathered from matings in which the fertility of both parents is unknown, and f_2 is estimated from another set of data gathered from matings in which the fertility of only the female parent is unknown. The significance of the difference of these two f values from zero can be tested by the standard deviation method. Thus, if the standard deviation of f_1 is S_{f_1}, and that of f_2 is S_{f_2}, and if the two sets of data are independent, then the standard deviation of $(f_1 \pm f_2)$ is:

$$S_{f_1 \pm f_2} = \sqrt{S^2_{f_1} + S^2_{f_2}},$$

where S_{f_1} and S_{f_2} are shown in equations (3) and (5), respectively. Hence the difference between $(f_1 - f_2)$ and zero in terms of the standard deviation of $(f_1 - f_2)$ is:

$$t = \frac{f_1 - f_2}{\sqrt{S^2_{f_1} + S^2_{f_2}}}$$

and the probability associated with any t value can be obtained from a table of the normal distribution.

If these two f values differ statistically as tested by the standard deviation method, then let f' be the probability of a female being fertile, and substitute it in equation (1):

$$f f' = \frac{b}{n_1}$$

or

$$f = \frac{b}{f'n_1}. \qquad (6)$$

Since b, n_1, and f' are known, equation (6) is readily solved for f, which is the probability of an individual male being fertile. But f and f' are not obtained independently and there are no means of testing whether the difference between f and f' is significantly different from zero. When these two f values are known, all the other equations with the exception of (7) and (8) can be readily solved.

In my experiments, except for the matings of blandus, two separate sets of data are not available. It is assumed that f and f' are of the same magnitude, and therefore the prime of f will be dropped in the following equations.

If there are two separate sets of data for any kind of matings, and if f can not be shown to differ in the two sets, it is logical to pool them to obtain a combined estimate of f by the maximum likelihood method.

Now, the joint probability, P, of obtaining precisely b fertile matings among n_1 matings when both parents are of unknown fertility and c fertile matings among n_2 matings when the male parent is known to be fertile is:

$$P\left({}^{b}/_{n_1}, {}^{c}/_{n_2}\right) = \left[\binom{n_1}{b} (f^2)^b \,(1-f^2)^{n_1-b}\right]\left[\binom{n_2}{c} (f)^c \,(1-f)^{n_2-c}\right].$$

Intuitively, the best estimate of f is that value which maximizes P, that is, that estimate which makes most probable the observed sampling distribution. Now

$$\log P = \log K_1 + b\log f^2 + (n_1 - b)\log(1-f^2) + \log K_2 + c\log f + (n_2 - c)\log(1-f)$$

where

$$K_1 = \binom{n_1}{b}$$

$$K_2 = \binom{n_2}{c}$$

and both are constants depending on the coefficients of the likelihood term.

Maximizing this logarithm gives:

$$\frac{d\log P}{d f} = \frac{2b}{f} - 2\,\frac{(n_1 - b)f}{1-f^2} + \frac{c}{f} - \frac{n_2 - c}{1-f} = 0 \qquad (7)$$

Equation (7) is a quadratic equation and is easily solved for f. The standard deviation of the maximum likelihood statistic f (Mather, 1951) is:

$$S_f = \sqrt{\frac{f(1-f^2)}{4n_1 f + n_2(1+f)}}\,. \qquad (8)$$

When the probability of individual fertility of each parent stock is known, the reproductive isolation index of the intersubspecific and interspecific crosses may be evaluated. Let f_a and f_b be the probabilities of individual fertility for two parent stocks A and B, respectively, and f^2_{ab} the proportion of fertile matings among the total cross matings of the type female stock A times male stock B. If no disturbing factors are involved, such as psychologic or gametic isolation, one would expect:

$$f^2_{ab} = f_a f_b \, .$$

The reproductive isolation index may now be defined as the ratio of the difference between the product of the two probabilities of individual fertility for two parent stocks and the observed proportion of fertile matings among the total cross matings to the sum of these two quantities. Therefore, if one measures the reproductive isolation between the female stock A and male stock B, the formula is:

$$I_{ab} = \frac{f_a f_b - f^2_{ab}}{f_a f_b + f^2_{ab}} \, . \tag{9}$$

Here $f_a f_b$ is used in both the numerator and the denominator to account for the effect of captivity in the laboratory. Although the laboratory conditions may be made as suitable to the animals as possible, they are never perfect, and the fertility of one stock might be more influenced by captivity than that of the other. One would, therefore, expect the fertility of cross matings to be affected in varying degrees according to the parent stocks used. In other words, cross fertility is a function of the probabilities of individual fertility in the two parent stocks. If, therefore, the proportion of fertile matings in an outcross is equal to the product of the two probabilities of individual fertility of two parent stocks, the reproductive isolation index is equal to zero. In all other cases the values may fluctuate in either direction, but it is easily seen that the values are bounded between -1.0 and +1.0. If all cross matings are sterile, the value of the index is +1.0. If negative values of the index are obtained, cross mating occurs in preference to matings between individuals of the same stocks.

Similarly, to measure the reproductive isolation of the reciprocal cross, i.e., the mating between female stock B and male stock A, the equation is:

$$I_{ba} = \frac{f_b f_a - f^2_{ba}}{f_b f_a + f^2_{ba}} \, . \tag{10}$$

Finally, these two types of reciprocal matings may be combined, and their joint reproductive isolation index, $I_{(ab)}$, measured The formula is:

$$I_{(ab)} = \frac{f_a f_b - f^2_{(ab)}}{f_a f_b + f^2_{(ab)}} \tag{11}$$

where $f^2_{(ab)}$ is the proportion of fertile matings in both reciprocal crosses of stocks A x B. In using this formula, it is desirable that the number of matings in the two reciprocal crosses be equal. The effect on the reproductive isolation index of marked departures from equality in the number of matings in the two reciprocal crosses has not been explored.

The statistical significance of departures of the observed values from the expected values, that is, $f_a f_b$, can readily be tested by chi-square as shown by Table I.

TABLE I

Scheme for Chi-square Test

Mating	Fertile Matings		Sterile Matings	Chi-square	d.f.
Cross between female stock A and male stock B	Observed	b	$n_1 - b$	$\frac{(b - n_1 f_a f_b)^2}{n_1 f_a f_b (1 - f_a f_b)}$	1
	Expected	$n_1 f_a f_b$	$n_1 (1 - f_a f_b)$		
Cross between female stock B and male stock A	Observed	c	$n_2 - c$	$\frac{(c - n_2 f_b f_a)^2}{n_2 f_b f_a (1 - f_b f_a)}$	1
	Expected	$n_2 f_b f_a$	$n_2 (1 - f_b f_a)$		
Both reciprocal crosses	Observed	$b + c$	$n_1 + n_2 - b - c$	$\frac{[(b+c) - (n_1+n_2) f_a f_b]^2}{(n_1+n_2) f_a f_b (1 - f_a f_b)}$	1
	Expected	$(n_1+n_2) f_a f_b$	$(n_1 + n_2)(1 - f_a f_b)$		

Analysis of Chi-square

Item	Chi-square	d.f.
Total	Sum of two χ^2's for two reciprocal crosses	2
Deviation	χ^2 from the item of both reciprocal crosses	1
Heterogeneity	Total χ^2 minus deviation χ^2	1

From Table I two kinds of chi-square are obtained for comparison. One is the total chi-square, which is obtained from the sum of two chi-squares for two reciprocal crosses, and the other is the deviation chi-square, which is obtained directly from the item of both reciprocal crosses. The difference between these two chi-squares is the heterogeneity chi-square, which is used to test the agreement of the two reciprocal crosses. The analysis is presented in tabular form. Details will be given later in the numerical analysis.

ANALYSIS OF DATA

The results of breeding within each of the three parent stocks, namely, P. p. leucocephalus, P. m. blandus, and P. m. bairdi, are summarized in Table II.

In these parent stocks the probability of individual fertility is highest

TABLE II

Probability of Individual Fertility in Three Parent Stocks of Peromyscus

Mating	Fertility of Both Sexes Unknown					Fertility with Males Known Before They Are Mated			
	Fertile Matings (b)	Sterile Matings $(n_1 - b)$	Total (n_1)	Proportion of Fertile Matings Among the Total (f^2)	Probability of Individual Fertility (f) and its Standard Deviation (s_f)	Fertile Matings (c)	Sterile Matings $(n_2 - c)$	Total (n_2)	Probability of Individual Fertility (f) and its Standard Deviation (S_f)
P. p. leucocephalus	9	20	29	0.31	0.56 ± 0.08	. . .	. . .	. . .	. . . . . .
P. m. blandus	28	4	32	0.88	0.94 ± 0.03	18	3	21	0.86 ± 0.08
P. m. bairdi	42	45	87	0.48	0.69 ± 0.04	. . .	. . .	. . .	. . . . . .

in blandus. The probability value of blandus is 0.94, that of bairdi is 0.69, and that of leucocephalus is low, only 0.56. The wide difference in the probability of individual fertility among these three parent stocks suggests that, among other things, the laboratory conditions were more favorable to the blandus stock than to the others.

In the case of blandus, data from two separate sets of matings are available, namely, one set from matings in which the fertility of both sexes is unknown, and another from the matings in which the fertility of the males is known from previous matings. The fertility in these two sets of matings, as measured by their f values, is not significantly different statistically ($t = 0.94$, $P = 0.40-0.30$). The best estimation of the f value may be obtained by applying the maximum likelihood method (equation 7), with the following results:

$$\frac{2(28)}{f} - \frac{2(4)f}{1 - f^2} + \frac{18}{f} - \frac{3}{1 - f} = 0.$$

The solution of this equation gives an f value of 0.91, and substitution of this f value in equation (8) gives $S_f = 0.03$. Since this probability of individual fertility and its standard deviation are obtained from the combined estimation of two sets of data, these values will be used for blandus in later calculations.

TABLE III

Reproductive Isolation Index of Certain Intersubspecific and Interspecific Crosses in Peromyscus

Mating	Fertile Matings	Sterile Matings	Total	Proportion of Fertile Matings Among Total (f^2)	Reproductive Isolation Index (I)
♀ P. p. leucocephalus x ♂ P. m. blandus	10	54	64	0.16	0.52
♀ P. m. blandus x ♂ P. p. leucocephalus	10	21	31	0.32	0.23
Both reciprocal crosses	20	75	95	0.21	0.42
♀ P. m. bairdi x ♂ P. m. blandus	14	33	47	0.30	0.35
♀ P. m. blandus x ♂ P. m. bairdi	34	11	45	0.76	-0.10
Both reciprocal crosses	48	44	92	0.52	0.09

Since the probability of individual fertility in the three parent stocks is known, equations (9), (10), and (11) are used to derive reproductive isolation indices for the intersubspecific and interspecific crosses. Their results are shown in Table III, and their chi-square values are shown in Tables IV and V, respectively.

TABLE IV

Chi-square Test for Reproductive Isolation in Crosses between P. p. leucocephalus and P. m. blandus

Mating	Fertile Matings	Sterile Matings	Total	χ^2	d. f.	P
♀ P. p. leucocephalus	Observed 10	54	64			
x				31.97	1	<0.01
♂ P. m. blandus	Expected 32.61	31.39	64			
♀ P. m. blandus	Observed 10	21	31			
x				4.34	1	0.05-0.02
♂ P. p. leucocephalus	Expected 15.80	15.20	31			
Both reciprocal	Observed 20	75	95			
crosses				33.99	1	<0.01
	Expected 48.41	46.59	95			

Analysis of Chi-square

Item	χ^2	d. f.	P
Total	36.31	2	<0.01
Deviation	33.99	1	<0.01
Heterogeneity	2.32	1	0.20-0.10

The reproductive isolation index between ♀ leucocephalus and ♂ blandus is quite high. Its value, 0.52, is statistically significant. The reproductive isolation index of the reciprocal cross is only 0.23, which is barely significant (P = 0.05-0.02). The joint reproductive isolation index of the two reciprocal crosses is 0.42, which, again, is statistically significant. Finally, the heterogeneity test shows that the data from these two reciprocal crosses are homogeneous.

The over-all picture given by these figures indicates that a certain amount of reproductive isolation has developed between leucocephalus and blandus, but that the degree of reproductive isolation is somewhat different in the reciprocal crosses. These two species occupy different geographic areas and ecologic niches with no naturally interbreeding intermediates. Since there is no chance for gene exchange between them in nature, genetic differences presumably have accumulated, and gradually reproductive isolation has been built up. In addition, leucocephalus is smaller in body size. When this species is used as the female parent in the cross, difficulty frequently arises in parturition (Watson, 1942).

It has been found that over half of the leucocephalus mothers died with their fetuses, but such high mortality does not occur if the larger blandus is used as the female parent. This is one of the facts which give an explanation of the difference of reproductive isolation indices between these two reciprocal crosses.

Reproductive isolation between blandus and bairdi presents different statistics. The reproductive isolation index of the cross between ♀ bairdi and ♂ blandus is 0.35, which is statistically significant, and that of the reciprocal cross is -0.10, statistically nonsignificant, whereas the joint reproductive isolation index of the two reciprocal crosses is 0.09, barely significant (P = 0.05-0.02). The chi-square test for heterogeneity shows that the fertility is different in the two reciprocal crosses.

TABLE V

Chi-square Test for Reproductive Isolation in Crosses between P. m. blandus and P. m. bairdi

Mating	Fertile Matings	Sterile Matings	Total	χ^2	d. f.	P
♀ P. m. bairdi x ♂ P. m. blandus	Observed 14	33	47	21.91	1	<0.01
	Expected 29.51	17.49	47			
♀ P. m. blandus x ♂ P. m. bairdi	Observed 34	11	45	3.13	1	0.10-0.05
	Expected 28.26	16.74	45			
Both reciprocal crosses	Observed 48	44	92	4.44	1	0.05-0.02
	Expected 57.77	34.23	92			

Analysis of Chi-square

Item	χ^2	d. f.	P
Total	25.04	2	<0.01
Deviation	4.44	1	0.05-0.02
Heterogeneity	20.60	1	< 0.01

These findings indicate that some reproductive isolation between bairdi and blandus probably exists, but that the joint reproductive isolation in the two reciprocal crosses is negligible (0.09). If one inspects the geographic distribution patterns of these two subspecies, it is found that intermediate interbreeding forms exist (Osgood, 1909). These facts coincide with the Laboratory findings that reproductive isolation between these two subspecies is negligible. But there is a significant heterogeneity, i.e., the fertility of the two reciprocal crosses is not the same. The question arises, therefore, of why a particular cross between bairdi and blandus shows reproductive isolation but the reciprocal does not. This is a difficult question to answer. Nevertheless, a clue may be found in the difference in individual fertility of the two parent stocks. It seems likely that the female may play a more important role in reproductive isolation than the male. To demonstrate whether this is true or not will require further experiments.

SUMMARY

Several simple formulae are presented for the measurement of fertility within and between parent stocks. The probability of individual fertility (f) of a parent stock, on which all other calculations depend, is equal to the square root of the proportion of b fertile matings among the total n_1, when the fertility of both sexes is unknown, or

$$f = \sqrt{\frac{b}{n_1}},$$

and is equal to the proportion of c fertile matings among the total n_2, when one sex is known to be fertile from a previous mating, or

$$f = \frac{c}{n_2}.$$

The reproductive isolation index is used to measure the reproductive isolation quantitatively and is defined as the ratio of $(f_a f_b - f^2_{ab})$, the difference between the product of the two probabilities of individual fertility for two parent stocks and the observed proportion of fertile matings among the total cross matings, to $(f_a f_b + f^2_{ab})$, the sum of these two quantities, or

$$I_{ab} = \frac{f_a f_b - f^2_{ab}}{f_a f_b + f^2_{ab}}.$$

The statistical significance of the departures of the observed values from the expected values is ascertained by the chi-square test.

The probabilities of individual fertility thus obtained are quite different in the three parent stocks studied. It is highest in Peromyscus maniculatus blandus (0.91), lower in P. m. bairdi (0.69), and lowest in P. polionotus leucocephalus (0.56). This probably means that, among other things, the laboratory conditions were more favorable to blandus than to leucocephalus.

The reproductive isolation indices of the cross leucocephalus x blandus and of its reciprocal cross are rather high (0.52 and 0.23), hence their joint reproductive isolation index is also high (0.42) and statistically significant. This shows that some reproductive isolation exists between these two species. The reproductive isolation indices of the cross bairdi x blandus and its reciprocal are either low or negative (0.35 and -0.10); in turn, the joint reproductive isolation index is very small (0.09) and statistically barely significant. This indicates that the reproductive isolation between these two subspecies is negligible.

LITERATURE CITED

DICE, L. R.

1933 Fertility relationships between some of the species and subspecies of mice in the genus Peromyscus. Journ. Mammalogy, 14: 298-305.

1947 Deer mice: methods for the rearing of Peromyscus. In: The UFAW handbook on the care and management of laboratory animals. London: Bailliere, Tindall & Cox. Pp. 171-77.

MATHER, K.

1951 The measurement of linkage in heredity. 2d ed.; London: Methuen & Co.

OSGOOD, W. H.

1909 Revision of the mice of the American genus Peromyscus. U. S. Dept. Agric., N. Amer. Fauna, 28: 1-285.

WATSON, M. L.

1942 Hybridization experiments between Peromyscus polionotus and Peromyscus maniculatus. Journ. Mammalogy, 23: 315-16.

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price, $0.20.

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

University of Michigan, Ann Arbor, Michigan

Number 60 February, 1953

PRENATAL MORTALITY IN PEROMYSCUS WITH SPECIAL REFERENCE TO ITS BEARING ON REDUCED FERTILITY IN SOME INTERSPECIFIC AND INTERSUBSPECIFIC CROSSES*

By T. T. LIU

Accepted for publication September 15, 1952

CONTENTS

Introduction 1
Materials and Methods 3
Prenatal Mortality in Parent Stocks 3
Prenatal Mortality in Intersubspecific Crosses 7
Prenatal Mortality in Interspecific Crosses 11
Prenatal Mortality and Maternal Age 13
Prenatal Mortality and Inbreeding 17
Resorbed Embryos and Sexes 23
Discussion 26
Summary 29
Literature Cited 30

INTRODUCTION

THE study of sterility in hybridization has occupied the attention of biologists for many years. Numerous investigations have demonstrated a wide range of mechanisms responsible for the reduced fertility. These mechanisms include: (1) sexual isolation, copulation not occurring because of the lack of mutual attraction of different forms; (2) mechanical isolation, copulation being difficult on account of the physical incompatibilities of the reproductive organs; (3) gametic isolation, spermatozoa failing to reach the eggs or to penetrate into the eggs; and (4) inviability of the hybrids, fertilization having taken place, with death of the zygote at some stage of development (Dobzhansky, 1941). It is apparent that the relative importance of these mechanisms depends on the kind of animals concerned and also on the relationship between the mating partners.

---

*A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

The genus Peromyscus, the common deermouse, is divided into many species groups, species, and subspecies. As a rule, a limited number of intersubspecific and interspecific crosses may occur within each species group (Dice, 1933). Hence, the animals are suitable for a study of some of the mechanisms responsible for hybrid sterility. Liu (1953) and Clark and Liu (MS) have analyzed the fertility relationships of three forms of mice from the Peromyscus maniculatus species group. The criterion of fertility in these studies was the number of living young born per mated female. It was found that in the intersubspecific crosses fertility was of the same order of magnitude as that of both parent stocks, but in the interspecific crosses the average fertility was much reduced.

The differences observed in fertility in different crosses are necessarily the result of the action of one or more of the four mechanisms listed above. Blair and Howard (1944) have studied sexual isolation within a species group and have reported that sterility in hybridization parallels the sexual isolation between parent stocks. The importance of the other three mechanisms in Peromyscus remains to be investigated.

It is known that early prenatal mortality in mammals, due either to the failure of some of the liberated ova to be fertilized or to complete resorption of the zygotes or early embryos, is indicated by a discrepancy between the number of corpora lutea in the ovaries and the total number of embryos in the uterine horns. Later embryonic inviability is indicated by the presence of embryonic remnants (Brambell and Mills, 1948). The study of the relative importance of the various mechanisms involved in the partial sterility of mammalian hybridization may be reduced to the investigation of prenatal mortality, which is here defined as mortality occurring at any stage of the developing organism prior to birth, including the unfertilized ovum. The purpose of this paper is to present some results of a study of prenatal mortality.

Acknowledgments

I wish to express my appreciation to Dr. James V. Neel for his helpful advice and guidance throughout this investigation. Thanks are also due Dr. Lee R. Dice and Dr. William J. Schull for their valuable suggestions and criticisms in reading the manuscript. The photographs were taken by Mr. William B. McIntosh to whom I am greatly indebted. The Institute of Human Biology, University of Michigan, has provided the necessary equipment for this study and has been responsible for the care of the laboratory animals.

MATERIALS AND METHODS

All the mice used in this study belong to the Peromyscus maniculatus species group.

Peromyscus maniculatus bairdi, from Washtenaw County, Michigan. — Stock collected by Van T. Harris, 1946.

Peromyscus maniculatus blandus, from Tularosa, Otero County, New Mexico. — Stock collected by W. F. and F. A. Blair, 1938.

Peromyscus polionotus leucocephalus, from Santa Rosa Island, Florida. — Stock collected by W. Frank Blair, 1942.

The subspecies bairdi is restricted to a prairie habitat. It is relatively small and light-bodied, with a buff and gray coloration. The subspecies blandus is found in a desert habitat. It is comparatively large and heavy-bodied with color more vinaceous. The geographic ranges of these two subspecies do not meet, but the two are connected by geographically and morphologically intermediate forms. The species polionotus is geographically isolated from the species maniculatus by a gap of several hundred miles where neither species occurs (Osgood, 1909). Leucocephalus is considerably smaller than either bairdi or blandus. It is very pale and lives in beach dunes.

The animals utilized in the present investigations have been reared by the methods described by Dice (1947). For each test mating a pair of sexually mature mice was isolated in a cage for six months to one and one-half years, or until the female was sacrificed, whichever occurred first. Matings with the relationship closer than first cousin and those in which the age of the female was greater than 83 weeks were excluded, except as otherwise mentioned. All matings were examined for litters or pregnancies every day until the female was killed. Pregnant females were killed at a late stage of gestation, usually one or two days from their full term. With experience this stage of gestation can readily be determined by simple palpation of the abdomen. The number of corpora lutea in each ovary was counted under a binocular dissecting microscope. The uteri were soaked in tap water in order to reveal "moles" (partly resorbed embryos and placentas) more clearly and also to prevent the uteri and their contents from drying out. The relative position in the uterus of each embryo was recorded and the sexes were identified if they were normally developed.

In the descriptions of the intersubspecific and interspecific crosses the female parent is named first; in the $F_1 \times F_1$ matings the various possible combinations are not considered separately but are treated as one, since they can not be shown to be different statistically in relation to prenatal mortality.

PRENATAL MORTALITY IN PARENT STOCKS

During pregnancy only one conspicuous set of corpora lutea is found in the ovary. This set is formed from the follicles which rupture at the ovulation preceding conception. Except in rare cases, when polyovulation or anovulation occurs, the corpora lutea of pregnancy offer the most reliable measure of ovarian activity (MacDowell, 1924). The numbers of corpora lutea and of normal fetuses in pregnant females of the three stocks, Peromyscus maniculatus bairdi, P. m. blandus, and P. poliononotus leucocephalus, are given in Table I and are illustrated in Figure 1.

Although the order of ovarian activity, as revealed by the average number of corpora lutea of pregnancy per female, is bairdi > blandus > leucocephalus, none of the differences between strains in this respect reaches the level of significance.

TABLE I

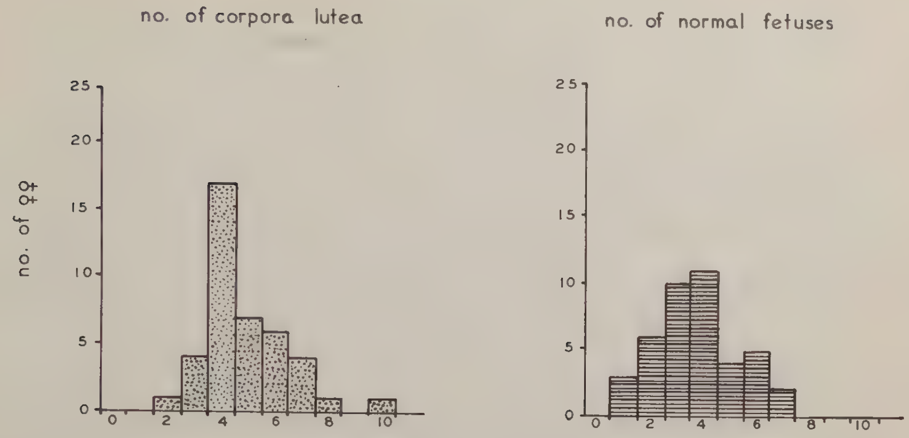
Number of Corpora Lutea and of Normal Fetuses in Three Parent Stocks

Stock	Number of ♀♀ Examined	Number of Corpora Lutea per Pregnant Female (Mean ± S. E.)	Number of Normal Fetuses per Pregnant Female (Mean ± S. E.)
P. m. bairdi	41	4.85±0.24	3.73±0.25
P. m. blandus	59	4.78±0.15	3.39±0.17
P. p. leucocephalus	5	4.60±0.24	2.80±0.49

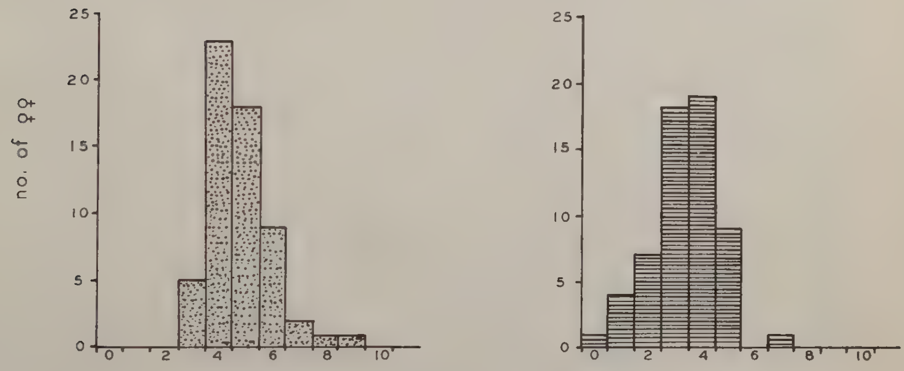
The number of normal fetuses per pregnant female shows the same trend. The value is greatest in bairdi, intermediate in blandus, and lowest in leucocephalus. Although the differences in the numbers of normal fetuses are greater than those in the numbers of corpora lutea, they still do not reach the level of significance.

The data of Table I show a higher number of corpora lutea than of normal fetuses. This discrepancy can only be explained by prenatal mortality. Prenatal mortality can be classified in three categories according to the developmental stage at which mortality occurs: (1) mortality occurring before or during implantation (corpora lutea not represented by embryos or embryonic remnants), (2) mortality occurring between a period shortly after implantation and approximately mid-term (partly resorbed embryos and placentas, which will be referred to henceforth as resorbed embryos), and (3) mortality occurring subsequent to mid-term (dead fetuses). The various values of these categories in the three parent stocks are summarized in Table II.

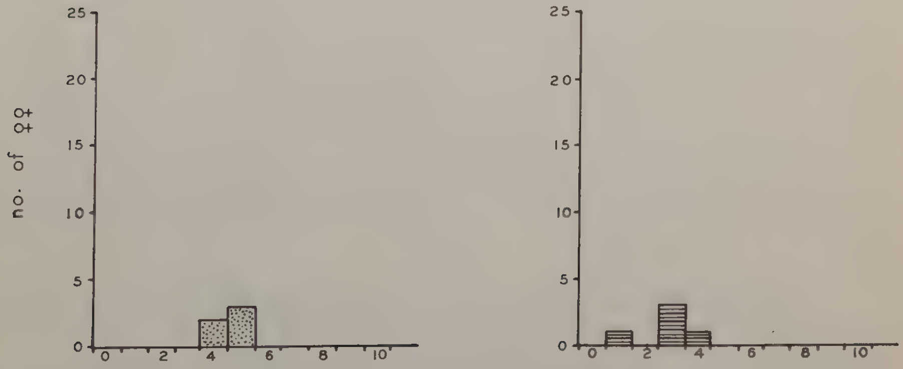
Mortality occurring before or during implantation may be due to any of the following causes: (1) liberated ova remain unfertilized; (2) ova are fertilized but fail to develop; or (3) ova are fertilized and develop up to approximately three days, then die and are completely resorbed. As no study of this early period of prenatal mortality was undertaken, the respective effects of these three causes were not distinguished. The category, "corpora lutea not represented by embryos," may therefore include any or all of these three factors. With respect to this



(a) P. m. bairdi



(b) P. m. blandus



(c) P. p. leucocephalus

Fig. 1. Number of corpora lutea and of normal fetuses in three parent stocks.

TABLE II

Prenatal Mortality in Three Parent Stocks

Stock	Number of Corpora Lutea	Total Number of Embryos	Number of Resorbed Embryos	Number of Dead Fetuses	Proportion of Corpora Lutea not Represented by Embryos	Proportion of Resorbed Embryos to Total Number of Embryos	Proportion of Dead Fetuses to Total Number of Embryos
P. m. bairdi	199	164	5	6	0.18±0.03	0.03±0.01	0.04±0.02
P. m. blandus	282	231	30	1	0.18±0.02	0.13±0.02	0.004±0.004
P. p. leucocephalus	23	16	2	0	0.30±0.10	0.13±0.08	0.00

category leucocephalus exceeds bairdi and blandus, which are somewhat similar in magnitude. Comparisons between two of each of these three stocks again show no statistical differences.

Although mortality can occur at any stage of gestation, all embryonic mortality noted in this study occurred at an early stage of development, except for a few cases in which the embryos were dead in a late gestational stage. In a few instances the resorbed embryos were represented either by partly resorbed placentas with remnants of embryonic membranes or by partly resorbed placentas with complete embryonic membranes in which the rudimentary embryo was located. In the majority of cases, however, the resorbed embryos were represented by a very small piece of tissue in which no placental tissue or embryonic tissue could be distinguished (Pl.I, Figs. 1 and 2).

The proportion of resorbed embryos to the total number of embryos is higher in blandus and leucocephalus, being 0.13±0.02 and 0.13±0.08, respectively, whereas in bairdi it is low, being only 0.03±0.01. Statistically, the proportion of resorbed embryos in blandus exceeds significantly that in bairdi (normal deviate c = 4.47, P less than 0.01), although the other two comparisons can not be shown to be different.

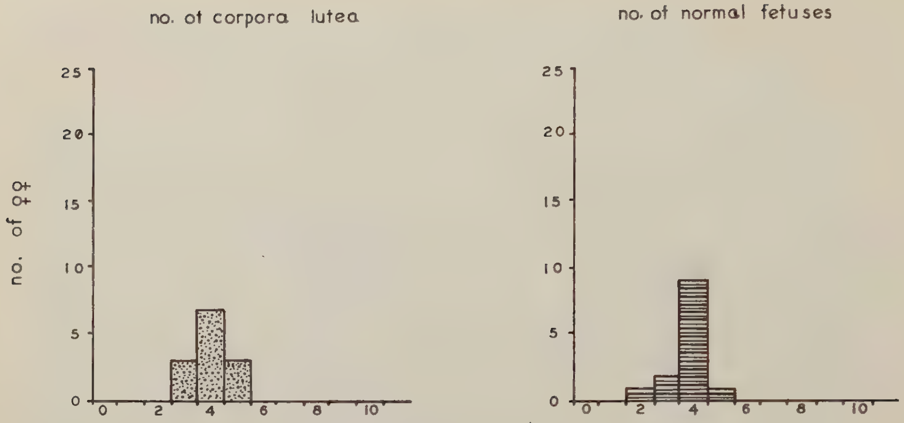
With respect to the dead fetuses, only one almost completely developed embryo has been found dead in the uterus of a blandus female. Since it occurred only once in 59 pregnant females which were examined, the proportion of dead fetuses is extremely low. Dead fetuses have also been found in bairdi, but they resulted from different causes. In one case, a female which had given birth to two young was found dead the next day. An autopsy revealed that the left uterine horn had two depressions, indicating that two placentas had been attached there, but that the right horn was still occupied by five fetuses. All the placentas of these five fetuses had been torn off from the uterine wall. The vagina of this pregnant female was twisted; hence the birth canal was blocked. In another instance one young had been born, and the female was found dead with another fetus retained in the uterus. Since this fetus appeared to be normal in all respects, the cause of the mishap remained unsolved. In bairdi, therefore, six fetuses died in the uterus at a late stage of development, and the proportion of dead fetuses to total embryo counts is 0.04±0.02. In leucocephalus, however, no dead fetus was found in the five females examined.

In summary it may be said that in these parent stocks embryos found dead at a late stage of gestation are extremely rare, and the deaths which do occur probably for the most part result from accidents incidental to parturition.

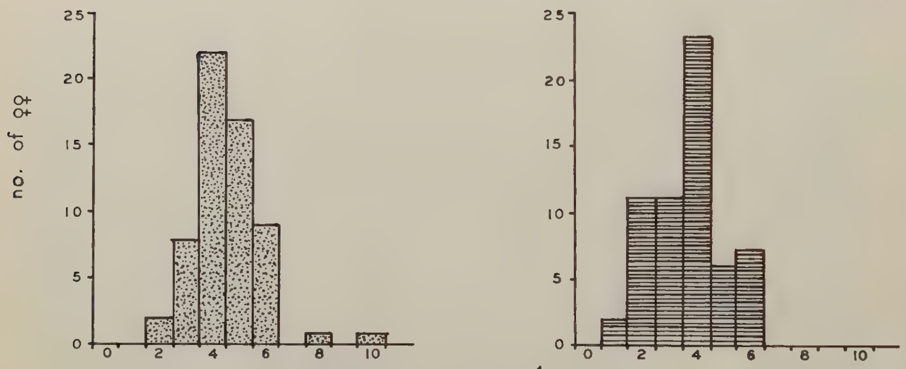
PRENATAL MORTALITY IN INTERSUBSPECIFIC CROSSES

The numbers of corpora lutea and of normal fetuses in the intersubspecific crosses between bairdi and blandus are given in Table III and are illustrated in Figure 2.

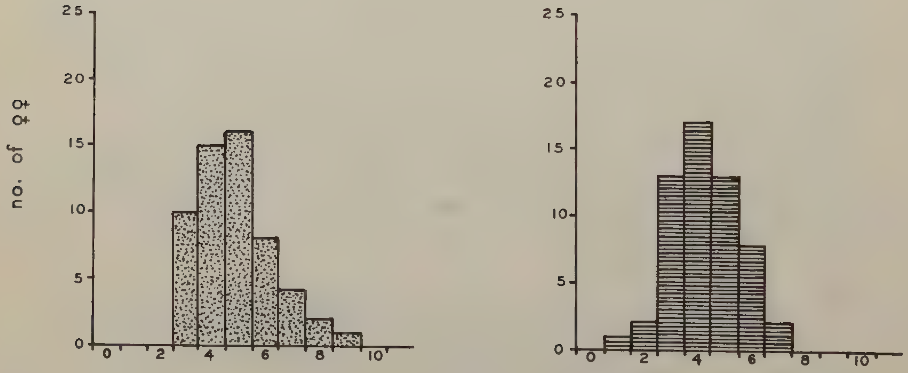
In the cross bairdi x blandus, the average number of corpora lutea



(a) ♀ P. m. bairdi x ♂ P. m. blandus



(b) ♀ P. m. blandus x ♂ P. m. bairdi



(c) $F_1 \times F_1$ (bairdi x blandus)

Fig. 2. Number of corpora lutea and of normal fetuses in intersubspecific crosses.

found in each pregnant female is 4.00±0.20, which is lower than that in bairdi inter se, but does not differ statistically (t=1.91, P=0.10-0.05). In the reciprocal cross blandus x bairdi, the number of corpora lutea is 4.55±0.17, which is close to that of the female parent stock. The average number of corpora lutea found in the F_1 x F_1 mating is 4.84 ±0.19, which is intermediate between that in the two parent stocks. The hybrid females, therefore, have the same ovarian activity as their parent stocks insofar as this is indicated by the number of corpora lutea.

TABLE III

Number of Corpora Lutea and of Normal Fetuses in Intersubspecific Crosses Between P. m. bairdi and P. m. blandus

Cross	Number of ♀♀ Examined	Number of Corpora Lutea per Pregnant Female (Mean ± S. E.)	Number of Normal Fetuses per Pregnant Female (Mean ± S. E.)
bairdi x blandus	13	4.00±0.20	3.77±0.20
blandus x bairdi	60	4.55±0.17	3.68±0.17
F_1 x F_1 (bairdi x blandus)	56	4.84±0.19	4.27±0.17

The average number of normal fetuses found in both reciprocal crosses is very close to the mean value of the two parent stocks. In the F_1 x F_1 mating, however, this value is higher and exceeds that in the cross blandus x bairdi (t=2.43, P=0.02-0.01), although it can not be shown to be different from that in the cross bairdi x blandus (t=1.36, P=0.20-0.10).

Since the number of normal fetuses in the crosses between bairdi and blandus is either close to or higher than that of the parent stocks, the prenatal mortality is necessarily low. Various categories of prenatal mortality are shown in Table IV. It is clearly seen that in both the reciprocal crosses the proportion of corpora lutea not represented by embryos is lower than that in both parent stocks. Their values are 0.04±0.02 and 0.13±0.02, respectively. The F_1 x F_1 mating shows the same trend, the value being intermediate to the crosses between bairdi and blandus.

The proportion of resorbed embryos parallels the proportion of corpora lutea not represented by embryos. Their values in the bairdi x blandus cross and in the F_1 x F_1 mating are very low; they are 0.02 ±0.02 and 0.02±0.01, respectively. The value in the blandus x bairdi mating is a little higher, but still lower than that in blandus inter se.

Dead fetuses were found only in an expectant female from the cross blandus x bairdi. In this instance the pregnant female was found dead after two young had been born. At autopsy, besides one resorbed embryo, two fetuses were found in the uterus, and a third fetus had entered the vagina. All these phenomena showed clearly that parturition was in progress. The cause of death is uncertain, but to judge from the

TABLE IV

Prenatal Mortality in Intersubspecific Crosses Between P. m. bairdi and P. m. blandus

Cross	Number of Corpora Lutea	Total Number of Embryos	Number of Resorbed Embryos	Number of Dead Fetuses	Proportion of Corpora Lutea not Represented by Embryos	Proportion of Resorbed Embryos to Total Number of Embryos	Proportion of Dead Fetuses to Total Number of Embryos
bairdi x blandus	52	50	1	0	0.04±0.02	0.02±0.02	0.00
blandus x bairdi	273	238	17	3	0.13±0.02	0.07±0.02	0.01±0.01
F_1 x F_1 (bairdi x blandus)	271	242	4	0	0.11±0.02	0.02±0.01	0.00

relatively large size of the fetuses, fetal-pelvic disproportion may have been a factor.

PRENATAL MORTALITY IN INTERSPECIFIC CROSSES

Since leucocephalus and blandus are assigned to different species, crosses between them are particularly interesting from the viewpoint of prenatal mortality. The numbers of corpora lutea and of normal fetuses are shown in Table V and are illustrated in Figure 3.

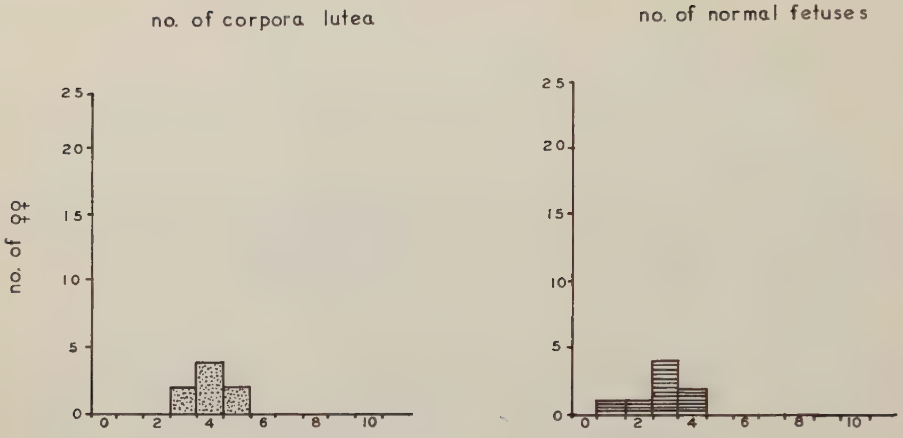
TABLE V

Number of Corpora Lutea and of Normal Fetuses in Interspecific Crosses Between P. m. blandus and P. p. leucocephalus

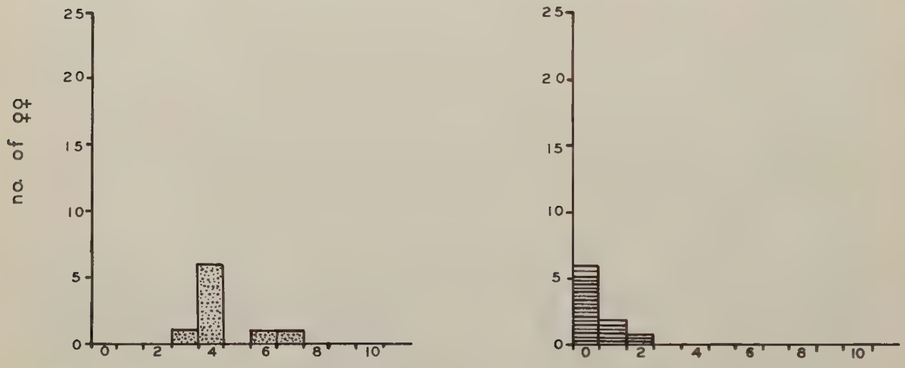
Cross	Number of ♀♀ Examined	Number of Corpora Lutea per Pregnant Female (Mean ± S. E.)	Number of Normal Fetuses per Pregnant Female (Mean ± S. E.)
blandus x leucocephalus	8	4.00±0.27	2.88±0.36
leucocephalus x blandus	9	4.44±0.13	0.44±0.08
F_1 x F_1 (blandus x leucocephalus)	22	4.55±0.21	3.32±0.24

The number of corpora lutea per pregnant female in the blandus x leucocephalus mating is 4.00±0.27, which is slightly lower than that in blandus mated inter se. As would be expected, the small discrepancy is probably due to sampling error (t=1.80, P=0.10-0.05). Since ovulation occurs spontaneously during estrum (Clark, 1936), there is no reason to suspect that the number of corpora lutea per pregnant female could be affected by the male stock used. The corpora lutea per pregnancy in leucocephalus x blandus is 4.44±0.13, which is close to that in leucocephalus mated inter se. In the F_1 x F_1 mating the value is 4.55 ±0.21, which is very close to the value of both parent stocks.

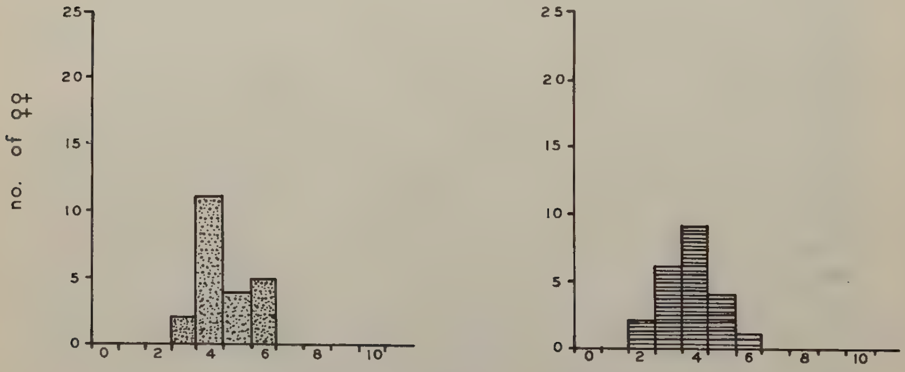
In the cross blandus x leucocephalus and its reciprocal the number of normal fetuses found per pregnancy is quite different, being 2.88±0.36 and 0.44±0.08, respectively. Because of this fact and because of a similar although less apparent difference in the intersubspecific crosses between bairdi and blandus, it is likely that the female parent has a more profound influence on prenatal mortality than has the male parent. The average number of normal fetuses in the cross blandus x leucocephalus falls more or less into the same magnitude as the values observed in both parent stocks, but the number in the leucocephalus x blandus cross is much lower and differs statistically from that of both parent stocks, blandus and leucocephalus (t=6.74 and t=4.88, P less than 0.01). The number of normal fetuses in the F_1 x F_1 mating is 3.32±0.24, which exceeds that in both parent stocks and in the F_1 hybrids.



(a) ♀ P. m. blandus x ♂ P. p. leucocephalus



(b) ♀ P. p. leucocephalus x ♂ P. m. blandus



(c) F_1 x F_1 (blandus x leucocephalus)

Fig. 3. Number of corpora lutea and of normal fetuses in interspecific crosses.

The cause of the wide difference in the numbers of normal fetuses in the reciprocal crosses is analyzed in Table VI. The proportions of corpora lutea not represented by embryos in the crosses blandus x leucocephalus and F_1 x F_1 (blandus x leucocephalus) are the same and are very close to those of the parent stocks. The proportions of resorbed embryos are also very similar in these two crosses and they resemble those of their parent stocks. Furthermore, dead fetuses were not discovered in these two crosses. On the other hand, the cross leucocephalus x blandus falls into an entirely different category. In this cross the proportion of corpora lutea not represented by embryos is very much higher (0.47 ± 0.08). It is different statistically from that in the cross blandus x leucocephalus and in F_1 x F_1 (the normal deviates $c = 3.10$ and $c = 3.47$, P being less than 0.01).

In addition to the high proportion of corpora lutea not represented by embryos, the cross leucocephalus x blandus resulted in a high proportion of dead fetuses. In one instance a female died one day after giving birth to a single offspring. At autopsy one abnormally large fetus was found in the vagina. It is thought that the disproportionally large size of the fetus may have been the cause of death. In five out of nine fertile matings the mice died close to term from a different cause. One or two days prior to death a viscous, hemorrhagic discharge appeared in the vaginal outlet. The mice moved very slowly and were not responsive to stimuli which usually evoke considerable activity. At autopsy serosanguineous fluid filled the cavity between the amniotic sacs and the uterine wall. Sometimes only one of the uterine horns was involved. Fetuses were usually two or three days from full term and appeared perfectly normal insofar as the external and internal morphology was concerned.

A few observations, made late in the course of the investigation, suggest that the size of placentas of the dead mice from the cross leucocephalus x blandus was greater than the size of the placentas of the normal mice from the cross blandus x leucocephalus (Pl.I, Figs. 3 and 4). Hence several measurements have been taken, the results of which are given in Table VII.

The mean value of the longest diameter of the placentas in the leucocephalus x blandus cross is 1.93 cm, which is statistically larger than the value in the blandus x leucocephalus cross, which is only 1.07 cm. The difference observed is not thought to be the result of postmortem changes. Because of this fact and also because of intra-uterine bleeding, it can be postulated that a placental overgrowth resulted in a disharmonious relationship between placental and maternal tissues. Further observations on this point are highly desirable.

PRENATAL MORTALITY AND MATERNAL AGE

There is an impression that when female mice reach a relatively advanced age the average litter size decreases. Since the genetic constitution of the female remains unchanged, one would expect either the

TABLE VI

TABLE VI

Prenatal Mortality in Interspecific Crosses
Between P. m. blandus and P. p. leucocephalus

Cross	Number of Corpora Lutea	Total Number of Embryos	Number of Resorbed Embryos	Number of Dead Fetuses	Proportion of Corpora Lutea not Represented by Embryos	Proportion of Resorbed Embryos to Total Number of Embryos	Proportion of of Dead Fetuses to Total Number of Embryos
blandus x leucocephalus	32	27	4	0	0.16±0.06	0.15±0.07	0.00
leucocephalus x blandus	40	21	0	17	0.47±0.08	0.00	0.81±0.09
F_1 x F_1 (blandus x leucocephalus)	100	84	11	0	0.16±0.04	0.13±0.04	0.00

number of ova liberated per estrous cycle to decrease or the prenatal mortality to increase with advance in maternal age.

In the two parent stocks, bairdi and blandus, the age of females examined ranged from a few months to more than two years. Hence, these mice were suitable for the present analysis. They have been arbitrarily divided into two age groups: (1) "prime" age, from sexual maturity to the age of 82 weeks (a little over one and one-half years old), and (2) "advanced" age, 83 weeks or older. Mice of the former group were used in the previous analysis, but mice of the latter group were not used. The data derived from the latter group are available for the analysis of maternal effect at an advanced age.

In this analysis the first step has been to determine whether or not the litter size actually decreases when the female mice reach an advanced age. In the preceding pages it has been shown that most prenatal mortality occurs at an early stage of development. Usually, the average litter size in mice is evaluated from the number of living young shortly after birth, but even by that time the young mice have been exposed to an early stage of postnatal mortality. The number of

TABLE VII

Length of the Longest Diameter of Placentas in Interspecific Crosses Between P. m. blandus and P. p. leucocephalus

Cross	Number of Placentas Measured	Mean Longest Diameter (cm)	t	P
leucocephalus x blandus	4	1.93	10.82	< 0.01
blandus x leucocephalus	6	1.07		

TABLE VIII

Relation of Litter Size to Two Age Groups in Two Parent Stocks, P. m. bairdi and P. m. blandus

All female mice were sacrificed one or two days before parturition.

Cross	Age Group	Number of ♀♀ Examined	Average Litter Size (Based on the Number of Normal Fetuses)
bairdi	Prime age	41	3.73
	Advanced age	11	3.45
blandus	Prime age	59	3.39
	Advanced age	21	2.05

normal late fetuses, which have survived the early stage of prenatal mortality and have not yet been exposed to any postnatal mortality, appears, therefore, to be the most reliable source for the estimation of average litter size. The values thus obtained and their statistical treatment (Brandt, 1933) are shown in Tables VIII and IX.

TABLE IX

Analysis of Variance for Litter Size in Relation to Age Groups in P. m. bairdi and P. m. blandus

Source	d.f.	Sum of Square	Mean Square	F	$F_{.05}$	$F_{.01}$
Stocks	1	17.12	17.12	9.56	....	6.84
Ages	1	22.34	22.34	12.48	....	6.84
Interaction (ages x stocks)	1	1.84	1.84	1.03	3.92	....
Error (between individual females)	128	229.76	1.79	....	....	....
Total	131	271.06				

Table IX, besides indicating that the litter size in bairdi exceeds that in blandus regardless of age, shows clearly that the litter size decreases with advancing age (F = 12.48, significant at the 1 per cent level). Tables X, XI, and XII contain an analysis of the factors responsible for this finding.

TABLE X

Relation of Corpora Lutea Counts to Two Age Groups in Two Parent Stocks, P. m. bairdi and P. m. blandus

Cross	Age Group	Number of ♀♀ Examined	Average Number of Corpora Lutea
bairdi	Prime age	41	4.85
	Advanced age	11	5.73
blandus	Prime age	59	4.78
	Advanced age	21	4.19

Table X shows that the corpora lutea counts do not differ significantly in relation to the two age groups. On the other hand, Table XII shows that when the females are of advanced age both bairdi and blandus have a higher proportion of corpora lutea which are not represented by embryos. The values for the advanced age in bairdi and blandus are 0.29 and 0.34, respectively, and the values for the prime age are lower, both 0.18. The proportion of resorbed embryos to total corpora lutea shows the same trend. In bairdi the proportion of resorbed embryos in the advanced age is 0.11, and that in the prime age is only 0.03. In blandus the proportion of resorbed embryos in the advanced age is 0.17, and that in the prime age is 0.11. The chi-square test shows that these figures are statistically different. Finally, the heterogeneity chi-square is found to be very low. The two sets of data, one from bairdi and the other from blandus, thus agree. By the method of partition of chi-square one may test which of these two factors, namely, corpora lutea not represented by embryos, and resorbed embryos, is more responsible for the higher prenatal mortality in advanced age. Tables XIII and XIV show that both the items "normal fetuses vs. corpora lutea not represented by embryos" and "normal fetuses vs. resorbed embryos" are significantly different in two age groups in bairdi and in blandus. It may be said, therefore, that when the female mice reach an advanced age, the average number of normal fetuses per pregnancy (or average litter size) decreases. This decrease is apparently not due to the release of fewer eggs at ovulation, as judged by the number of corpora lutea, but is a consequence both of a higher proportion of corpora lutea not being represented by embryos and of a higher proportion of those which develop embryos being partly resorbed.

TABLE XI

Analysis of Variance for Corpora Lutea Counts in Relation to Age Groups in P. m. bairdi and P. m. blandus

Source	d.f.	Sum of Square	Mean Square	F	$F_{.05}$	$F_{.01}$
Stocks	1	17.18	17.18	8.42	....	6.84
Ages	1	0.10	0.10	0.05	3.92	....
Interaction (ages x stocks)	1	0.10	0.10	0.05	3.92	....
Error (between individual females)	128	260.68	2.04	....	....	....
Total	131	278.06				

PRENATAL MORTALITY AND INBREEDING

It has been shown that prenatal mortality in three stocks of Peromyscus differs in extent, although statistically significant differences

TABLE XII

Maternal Age in Relation to Prenatal Mortality in P. m. bairdi and P. m. blandus

Cross	Age Group	Number of ♀♀ Examined	Corpora Lutea not Represented by Embryos		Resorbed Embryos		Normal Fetuses		Total	χ^2	P
			Number	Proportion	Number	Proportion	Number	Proportion			
bairdi	Prime	41	35	0.18	5	0.03	153	0.79	193 } 256	12.14	<0.01
	Advanced	11	18	0.29	7	0.11	38	0.60	63		
blandus	Prime	59	51	0.18	30	0.11	200	0.71	281 } 369	15.05	<0.01
	Advanced	21	30	0.34	15	0.17	43	0.49	88		
Total	Prime	100	86	0.18	35	0.07	353	0.75	474 } 625	23.58	<0.01
	Advanced	32	48	0.32	22	0.14	81	0.54	151		

Analysis of Chi-square

Item	χ^2	d. f.	P
Total	27.19	4	<9.01
Deviation	23.58	2	<0.01
Heterogeneity	3.61	2	0.20-0.10

have not been demonstrated. That genetic factors, such as recessive lethal and semilethal genes, are partly responsible for the observed differences in prenatal mortality in various crosses is a possibility that may be explored. If such factors are operative, embryos resulting from matings of closely related individuals will have higher mortality than embryos from matings of less closely related or of unrelated individuals, because in the former these genes are more likely to occur in the homozygous condition causing death.

TABLE XIII

Partition of Chi-square of Table XII for Prenatal Mortality in Relation to Age Groups in P. m. bairdi

Source	χ^2	d.f.	P
Normal fetuses vs. resorbed embryos	8.99	1	<0.01
Normal fetuses + resorbed embryos vs. corpora lutea not represented by embryos	3.15	1	0.10-0.05
Total	12.14	2	<0.01

Source	χ^2	d.f.	P
Normal fetuses vs. corpora lutea not represented by embryos	4.42	1	0.05-0.02
Normal fetuses + corpora lutea not represented by embryos vs. resorbed embryos	7.72	1	<0.01
Total	12.14	2	<0.01

In the crosses blandus inter se, F_1 x F_1 (blandus x bairdi) and F_1 x F_1 (blandus x leucocephalus), data have been accumulated on the results of brother-sister matings in addition to the data on ordinary matings used in all previous analyses. Hence, each cross consists of two sets of data with respect to the kinds of relationships, namely, one set of data from the matings where the relationship of the partners was not closer than first cousin, as in blandus inter se, or where the partners were unrelated as in $F_1 \times F_1$ (blandus x bairdi) and $F_1 \times F_1$ (blandus x leucocephalus), and the other set of data from the matings where the relationship of partners was that of full sibs, although they may have belonged to different litters. Since it is desirable to make the maternal age as uniform as possible to reduce the maternal effect, only the results of the first pregnancy are used in the analysis.

For convenience of statistical treatment, the kinds of prenatal mortality, i.e., proportion of corpora lutea not represented by embryos and the proportion of resorbed embryos to total number of embryos, as well as their chi-square values, are shown separately in Tables **XV** and **XVI**.

TABLE XIV

Partition of Chi-square of Table XII for Prenatal Mortality in Relation to Age Groups in P. m. blandus

Source	χ^2	d.f.	P
Normal fetuses vs. resorbed embryos	5.11	1	0.05-0.02
Normal fetuses + resorbed embryos vs. corpora lutea not represented by embryos	9.94	1	<0.01
Total	15.05	2	<0.01

Source	χ^2	d.f.	P
Normal fetuses vs. corpora lutea not represented by embryos	12.51	1	<0.01
Normal fetuses + corpora lutea not represented by embryos vs. resorbed embryos	2.54	1	0.20-0.10
Total	15.05	2	<0.01

It is seen from Table **XV** that in matings of blandus inter se and of $F_1 \times F_1$ (blandus x leucocephalus) the number of corpora lutea not represented by embryos is higher in brother-sister matings, but conversely in the cross $F_1 \times F_1$ (blandus x bairdi) the number is higher in the unrelated matings. Hence, the results of different crosses are contradictory, although the chi-square tests show that these values are not significantly different.

TABLE XV

Proportion of Corpora Lutea not Represented by Embryos
in Relation to Degree of Inbreeding

Cross	Relationship Between Mating Partners	Corpora Lutea not Represented by Embryos		Corpora Lutea Represented by Embryos		Total	χ^2	P
		Number	Proportion	Number	Proportion			
blandus inter se	Brother-sister	10	0.19	44	0.81	54	0.87	0.50-0.30
	Not closely related	15	0.13	100	0.87	115		
F_1 x F_1 (bairdi x blandus)	Brother-sister	21	0.15	122	0.85	143	1.00	0.50-0.30
	Unrelated	25	0.19	105	0.81	130		
F_1 x F_1 (blandus x leucocephalus)	Brother-sister	5	0.33	10	0.67	15	0.81	0.50-0.30
	Unrelated	7	0.21	26	0.79	33		

TABLE XVI

Proportion of Resorbed Embryos in Relation to Degree of Inbreeding

Cross	Relationship Between Mating Partners	Resorbed Embryos		Normal Embryos		Total	χ^2	P
		Number	Proportion	Number	Proportion			
blandus inter se	Brother-sister	5	0.11	39	0.89	44	0.76	0.50-0.30
	Not closely related	7	0.07	93	0.93	100		
F_1 x F_1 (bairdi x blandus)	Brother-sister	13	0.11	109	0.89	122	5.24	0.05-0.02
	Unrelated	3	0.03	102	0.97	105		
F_1 x F_1 (blandus x leucocephalus)	Brother-sister	2	0.20	8	0.80	10	0.43	0.70-0.50
	Unrelated	3	0.12	23	0.88	26		
Total	Brother-sister	20	0.11	156	0.89	176	4.41	0.05-0.02
	Unrelated or not closely related	13	0.06	218	0.94	231		

Analysis of Chi-square

Item	χ^2	d. f.	P
Total	6.43	3	0.10-0.05
Deviation	4.41	1	0.05-0.02
Heterogeneity	2.02	2	0.30-0.50

On the other hand, Table XVI shows that the proportion of resorbed embryos to total number of embryos is higher in the brother-sister matings. The values of resorbed embryos are 0.11 in blandus, 0.11 in F_1 x F_1 (blandus x bairdi), and 0.20 in F_1 x F_1 (blandus x leucocephalus). In matings of blandus inter se and of F_1 x F_1 (blandus x leucocephalus), however, the sample sizes are not large enough to make the values in brother-sister matings differ statistically from those values in the matings which are not closely related. In F_1 x F_1 (blandus x bairdi) matings, the proportion of resorbed embryos in the brother-sister matings does differ statistically at the 5 per cent level ($\chi^2 = 5.24$) from that in the unrelated matings. The total chi-square turns out to be 4.41, which is significant at the 5 per cent level for one degree of freedom. As would be expected, the heterogeneity test shows that data on the proportion of resorbed embryos in these crosses are in agreement with each other ($\chi^2 = 2.02$, P=0.50-0.30).

The analysis given above indicates that close inbreeding probably has no significant effect on the proportion of corpora lutea not represented by embryos, but that it increases the number of resorbed embryos.

RESORBED EMBRYOS AND SEXES

There is an indication that in some animals, especially man, the frequency of abortive embryos is higher among male embryos than among female embryos. One of the several hypotheses by which an attempt is made to explain such a phenomenon states that sex-linked lethal and semilethal genes are responsible for the sex-differential mortality (Little and Gibbons, 1921, cited from Spuhler, 1948). In Peromyscus it has been shown that genetic factors play a role in the occurrence of resorbed embryos. It would then be interesting to know whether the occurrence of resorbed embryos is due mainly to autosomal lethal and semilethal genes, or whether sex-linked genes take an active part also. To demonstrate this it is necessary to divide each type of mating into two classes, one with and the other without resorbed embryos, and to analyze the difference in sex ratio with respect to these two classes. The data have been compiled for this purpose and are summarized in Table XVII.

In all of the crosses, except in bairdi x blandus and F_1 x F_1 (blandus x bairdi), the pregnancies in which there occurs one or more resorbed embryos show a higher number of males per female than do the pregnancies without resorbed embryos. For example, the value in the cross blandus x leucocephalus is 2.00 and that in the cross bairdi inter se is 1.62, whereas the respective values for the pregnancies without resorbed embryos are 0.47 and 0.85, although none of them shows a significant difference. The heterogeneity chi-square test indicates that the whole set of data is rather consistent. It may therefore be stated that sex-linked lethal and semilethal genes are not responsible for the occurrence of resorbed embryos in various crosses to any noticeable extent.

TABLE XVII

Proportion of Resorbed Embryos in Relation to Sex

Whenever the number of entries in a given class is four or less, either Yates' correction has been applied or the exact probability has been calculated (Fisher, 1948). The values thus obtained are put in parentheses.

Cross	Resorbed Embryos	Sex		Total	Number of Males per Female	χ^2	P
		Female	Male				
blandus	With	47	53	100	1.13	0.57	0.50-0.30
	Without	87	81	168	0.93		
bairdi	With	13	21	34	1.62	2.79	0.10-0.05
	Without	78	66	144	0.85		
leucocephalus	With	3	4	7	1.33	1.17	0.30-0.20
	Without	5	2	7	0.40	(0.29)	
bairdi x blandus	With	2	2	4	1.00	0.09	0.90-0.80
	Without	19	26	45	1.37	(0.05)	
blandus x bairdi	With	18	24	42	1.33	0.25	0.70-0.50
	Without	83	93	176	1.12		
blandus x leucocephalus	With	3	6	9	2.00	3.19	0.10-0.05
	Without	15	7	22	0.47	(1.92)	

leucocephalus x blandus	With	. . .	. . .	. . .	. . .	. . .	. . . .
	Without	. . .	. . .	. . .	. . .	. . .	. . . .
F_1 x F_1 (blandus x bairdi)	With	27	20	47	0.74	0.64	0.50-0.30
	Without	151	144	295	0.95		
F_1 x F_1 (blandus x leucocephalus)	With	15	15	30	1.00	0.60	0.50-0.30
	Without	30	21	51	0.70		
Total	With	128	145	273	1.13	1.82	0.20-0.10
	Without	468	440	908	0.94		

Analysis of Chi-square

Item	χ^2	d. f.	P.
Total	9.30	7	0.30-0.20
Deviation	1.82	1	0.20-0.10
Heterogeneity	7.48	6	0.30-0.20

DISCUSSION

The presence of resorbed or dead embryos in the uteri is direct evidence of prenatal mortality; however, the estimation of prenatal mortality from the discrepancy between the number of corpora lutea and the total number of embryos is subject to certain criticisms. As Hall and Davis (1950) have pointed out, some of the structures counted as corpora lutea may be Graafian follicles which do not release an ovum. In such cases the corpora lutea count is likely to be higher than the actual number of ova released. On the other hand, some follicles give rise to more than one ovum, that is, polyovulation occurs, and thus the intra-uterine mortality appears lower than it actually is. But in observation on serial sections of twenty-two ovaries of the parent stocks and of the hybrids in Peromyscus, neither Graafian follicles with more than one ovum nor luteinized follicles with trapped ova have been found. This appears to indicate that polyovular follicles and anovular luteinized follicles are comparatively rare, if present at all, in the females of this genus. The corpora lutea which are not represented by embryos, therefore, probably give a rather reliable estimation of the number of unfertilized ova and of completely resorbed embryos.

As the preceding analysis has shown, several factors influence prenatal mortality. Before conclusions can be reached concerning the amount of prenatal mortality in certain specific and subspecific crosses, it is necessary to demonstrate clearly that the observed differences are not due to variables, such as age or inbreeding, but are correlated with the taxonomic entities which are of particular concern in this paper.

The present observations reveal that when the mouse reaches a relatively advanced age, the average number of embryos per pregnancy decreases, both because of the higher proportion of corpora lutea which fail to be represented by embryos and also because a higher proportion of the developing embryos are partly resorbed. In this analysis it was not possible to hold the age of the male parents constant, but since it usually paralleled the age of the female parents, the decreased male fertility may be somewhat responsible for the increased proportion of corpora lutea not represented by embryos (Yerushalmy, 1939). It is apparent, however, that maternal effects are more important in this respect. Blandau and Jordan (1941) found a considerable increase in prenatal mortality in rats, particularly preimplantation loss, when fertilization was delayed a few hours. Whether delayed fertilization is a factor to be considered in natural matings is not known. Perhaps it may be encountered more often in old females. In addition, the intra-uterine environment may be less favorable for implantation and subsequent development in females of relatively advanced age. Hence, the embryos are more likely to die and to be resorbed. The validity of these suggestions can only be determined by further observations.

Genetic factors, either lethal or semilethal, are usually considered among the important causes of prenatal mortality in mammals. Corner (1923) believes that much of the prenatal mortality in the pig is due to genetic defects. He did not, however, have adequate genetic data to prove his statement. Hammond (1928, cited from Brambell, 1944) has reported that in an inbred strain of rabbits possibly several recessive genes operating through the mother are responsible for the fetal atrophy. But Hollander and Strong (1950) stated that in the house mouse (and probably also in the rat) the segregation of recessive lethal genes can not be an adequate genetic explanation of most of the mortality. On that basis one would expect very little mortality in the hybrid embryos of the crosses between different strains, whereas only a slight reduction in prenatal mortality in such crosses has been observed. From an analysis of the connection between mortality and closeness of relationship of mating partners, it has been clearly shown in Peromyscus that in brother-sister matings there is a general tendency to an increase in the mortality rate, especially among F_1 x F_1 (bairdi x blandus) hybrids. Since in the brother-sister mating the probability that the offspring will inherit the same semilethal or lethal genes from the female or male parent increases, a higher proportion of zygotes becomes homozygous for these recessive lethal genes, and consequently the number of resorbed embryos increases. The present observations, therefore, give strong evidence that genetic factors are partly responsible for the occurrence of prenatal mortality.

Evidence of sex-linked inheritance in rodents has thus far been limited to a few incompletely documented instances, mainly in house mice. This fact, plus cytological observations, has led White (1945) to the conclusion that the sex chromosome of rodents is composed mostly of heterochromatin and probably plays little part in the genetic control of morphogenetic processes, other than the determination of sex. Recently Hauschka, Goodwin, and Brown (1951) reported a sex-linked lethal gene in the house mouse. Falconer (1952) also has shown that the "tabby" in the house mouse is sex linked. Thus far no single sex-linked gene has been found in Peromyscus. Hence such genes, if they are present at all, would be very rare in Peromyscus. In the analysis of the relationship between resorbed embryos and sex ratio in Peromyscus, the pregnancies with resorbed embryos show an even higher proportion of males in comparison with the pregnancies without resorbed embryos, but all of the occurrences are not statistically significant. Hence, it may be said that sex-linked lethal and semilethal genes do not have any detectable effect on the prenatal mortality.

Thus far several possible causes of prenatal mortality have been discussed. It has been shown that increasing maternal age and close genetic relationship between mating partners tend to augment the incidence of prenatal mortality. Since all the matings used in the present study, except those used for particular purposes, such as to analyze the amount of inbreeding in relation to prenatal mortality, are of comparable age (i.e., all of prime age) and with relationship not closer than first cousin, these factors do not enter into the interpretation of the differences in prenatal mortality in various crosses.

The proportion of corpora lutea not represented by embryos and the proportion of resorbed embryos are low in the intersubspecific cross bairdi x blandus and a little higher in the reciprocal cross. In general, the mortality is comparable to that of parent stocks, as is also the mortality of the F_1 x F_1 mating. According to Osgood (1909), these two geographically isolated subspecies are connected by interbreeding forms. In the laboratory the fertility between these two subspecies is close to that existing in their parent stocks when no choice of mates is allowed. All these observations are compatible and indicate that the low prenatal mortality in these intersubspecific crosses is responsible for the high fertility between the two parent stocks.

In the interspecific crosses between blandus and leucocephalus the two reciprocal crosses show different tendencies with respect to prenatal mortality. In the cross blandus x leucocephalus the proportion of corpora lutea not represented by embryos and the proportion of resorbed embryos are close to those of the parent stocks, while in the cross leucocephalus x blandus, the situation is entirely different. The proportion of dead fetuses and the proportion of corpora lutea not represented by embryos are very high, but not one resorbed embryo has been found. The high proportion of dead fetuses is apparently due to increased inviability of hybrid zygotes, which may trace back to the disharmonious relationships between developing embryos and intrauterine environment, as has been pointed out. Although the mechanisms responsible for this "disharmony" are unknown, one obvious possibility involves a serological incompatibility, such as that illustrated by the Rh situation in man. Suppose that blandus is homozygous for a pair of dominant genes which are responsible for the production of an antigen, whereas leucocephalus lacks this gene. Then in the cross leucocephalus x blandus a recessive female would carry heterozygous fetuses and the antigen produced by the latter could penetrate the placenta, reach the body of a pregnant female, and cause the production of an antibody. When the antibody finds its way, again through the placenta, to the heterozygous fetuses, an immunological reaction occurs, resulting in the premature death of fetuses. It is easily seen that such reaction would not occur if blandus is used as the female parent. In order to determine the validity of this hypothesis, serological examination has been undertaken in two pregnant leucocephalus females which had been mated with blandus males. The serum obtained from these two leucocephalus mice failed to agglutinate the erythrocytes from blandus mice. Nevertheless, it is worth while to point out that if the hypothesis outlined above is the main factor responsible for the occurrence of dead fetuses in the cross leucocephalus x blandus, the same phenomenon should occur in some of the F_2 x F_2 matings because this particular gene pair would segregate in F_2 generation. With respect to this point, further experimental observations are highly desirable.

The high proportion of corpora lutea not represented by embryos is also worth further consideration. If it is assumed that most of the ova in the pregnant females from the cross leucocephalus x blandus were fertilized and began development but were completely resorbed later, some resorbed embryos should have been recovered. But since this was not the case, it is quite possible that a high proportion of liberated ova failed to be fertilized.

Two possible explanations of these findings deserve mention: (1) Since leucocephalus is considerably smaller in body size than blandus, mechanical isolation or physical incompatibility may have been responsible for a smaller quantity of spermatozoa being injected into the vagina. This, of course, could decrease the probability that a liberated egg would be fertilized. (2) Spermatozoa may have been injected into the cervix of the uterus but failed either to reach or to penetrate the ova. Either one or both of these factors can cause the failure of a larger proportion of corpora lutea to be represented by embryos.

Since leucocephalus and blandus are geographically isolated by a gap of several hundred miles where no intermediate forms exist, there is no opportunity for gene exchange between them in nature, genetic differences presumably have been accumulated, and gradually the sexual isolation between these two species has been developed (Blair and Howard, 1944). Even in the laboratory the fertility between the members of this particular cross, leucocephalus x blandus, is very low when no choice of mates is allowed, although in the reciprocal cross the fertility is higher (Liu, 1953; Clark and Liu, MS, Watson, 1942). These findings are fairly consistent with those of prenatal mortality, that is, increased prenatal mortality parallels high sterility. In other words, in the cross blandus x leucocephalus the fertility is comparable to that of the parent stocks: the proportion of corpora lutea not represented by embryos and the proportion of resorbed embryos are of the same magnitude as that of their parent stocks, but in the cross leucocephalus x blandus, the fertility is much reduced, a high proportion of liberated ova fails to be fertilized, and the viability of hybrid zygotes is considerably lower. It may be concluded, therefore, that, in addition to the existence of sexual isolation, the higher prenatal mortality of the crosses between blandus and leucocephalus substantiates the validity of assigning these two forms as separate species.

SUMMARY

1. Prenatal mortality has been studied with respect to three forms of the Peromyscus maniculatus species group and the two possible crosses between these forms.

2. From the examination of the ovaries and the uterine contents of a near-term, pregnant mouse, the stage of development at which prenatal death occurred can be estimated as follows: (a) mortality occurring before or during implantation (corpora lutea not represented by embryos or embryonic remnants), (b) mortality occurring between a period shortly after implantation and approximately mid-term (partly resorbed embryos and placentas), and (c) mortality occurring subsequent to mid-term (dead fetuses).

3. Prenatal mortality is not significantly different for P. maniculatus blandus, P. m. bairdi, and P. polionotus leucocephalus.

4. Fertility in the intersubspecific crosses between P. m. bairdi and P. m. blandus is comparable to that of the parent stocks, and the

proportion of corpora lutea not represented by embryos and the proportion of resorbed embryos are low.

5. In the interspecific crosses between blandus and leucocephalus the average fertility is reduced. This is due both to the fact that fewer liberated ova are fertilized in the pregnant female and to the fact that the proportion of dead fetuses is increased.

6. Prenatal mortality increases with the advance of maternal age.

7. Close inbreeding tends to augment prenatal mortality. This observation may be accounted for by the presence of autosomal lethal and semilethal genes. Inasmuch as no excess mortality was observed among male embryos, sex-linked lethal genes do not appear to play a significant role.

8. The parallelism between prenatal mortality and reduced fertility has been emphasized.

LITERATURE CITED

BLAIR, W. FRANK, and WALTER E. HOWARD

1944 Experimental evidence of sexual isolation between three forms of mice of the cenospecies Peromyscus maniculatus. Contrib. Lab. Vert. Biol. Univ. Mich., 26:1-19.

BLANDAU, R. J., and E. S. JORDAN

1941 The effect of delayed fertilization on the development of the rat ovum. Amer. Journ. Anat., 68:275-91.

BRAMBELL, F. W. R.

1944 Reproduction of wild rabbit, Oryctolagus cuniculus. Proc. Zool. Soc. London, 114:1-45.

BRAMBELL, F. W. R., and I. H. MILLS

1948 Studies on sterility and prenatal mortality in wild rabbits. IV. The loss of embryos after implantation. Journ. Exper. Biol., 25:241-69.

BRANDT, A. E.

1933 The analysis of variance in a "2 x s" table with disproportionate frequencies. Journ. Amer. Stat. Assoc., 28:164-73.

CLARK, FRANK H.

1936 The estrous cycle of the deer-mouse, Peromyscus maniculatus. Contrib. Lab. Vert. Genetics Univ. Mich., 1:1-7.

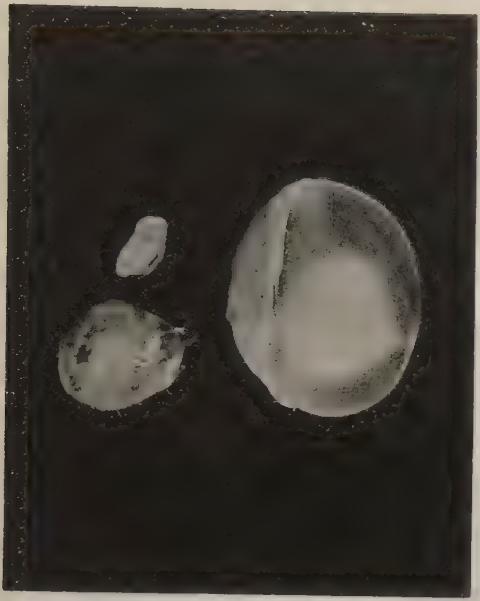
CLARK, PHILIP J., and T. T. LIU

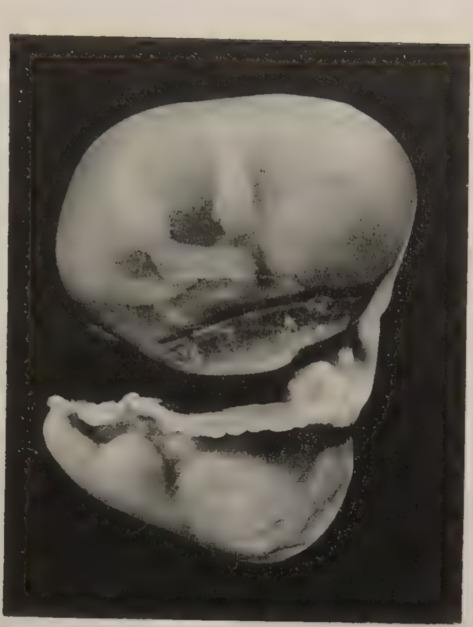
MS Postnatal mortality in some laboratory-bred Peromyscus.

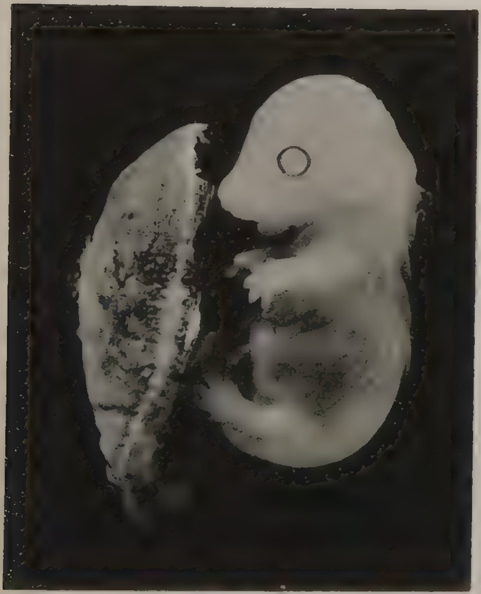
CORNER, G. W.

1923 The problem of embryonic pathology in mammals with observations upon intra-uterine mortality in the pig. Amer. Journ. Anat., 31:523-45.

PLATE I


1


2


3

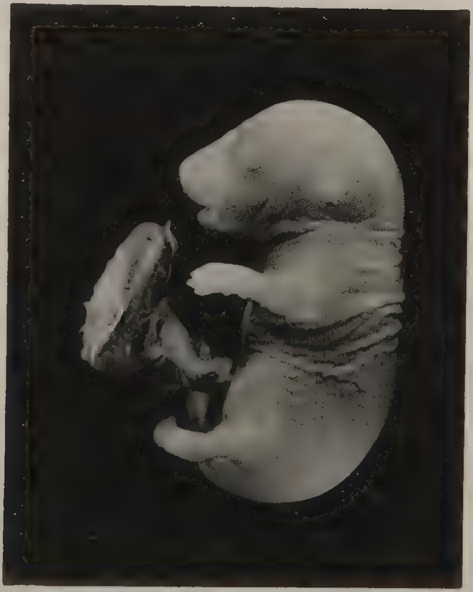

4

FIG. 1. Three resorbed embryos. Upper left, material in which no placental or embryonic tissues can be distinguished; lower left, partly resorbed placenta with remnant of embryonic membranes; right, partly resorbed placenta with complete embryonic membranes containing rudimentary embryo (all enlarged). FIG. 2. Preserved uterus: a normal fetus in one horn and two resorbed embryos in the other (enlarged). FIG. 3. Dead fetus from the cross P. polionotus leucocephalus × P. maniculatus blandus, showing the disproportionally large placenta (enlarged). FIG. 4. Fully developed fetus with normal placenta from the cross P. maniculatus blandus inter se (enlarged).

DICE, LEE R.

1933 Fertility relationships between some of the species and subspecies of mice in the genus Peromyscus. Journ. Mammalogy, 14:298-305.

1947 Deer mice. Methods for rearing of Peromyscus. In: The UFAW handbook on the care and management of laboratory animals. London: Bailliere, Tindall and Cox. Pp. 171-77.

DOBZHANSKY, THEODOSIUS

1941 Genetics and the origin of species. 2d ed.; New York: Columbia Univ. Press.

FALCONER, D. S.

1952 A totally sex-linked gene in the house mouse. Nature, 169:664.

FISHER, R. A.

1948 Statistical methods for research workers. 10th ed.; New York: Hafner Publishing Company.

HALL, OCTAVIA, and DAVID E. DAVIS

1950 Corpora lutea counts and their relation to the number of embryos in the wild Norway rat. Texas Rpts. on Biol. and Med., 8:564-82.

HAUSCHKA, THEODORE S., MARGARET B. GOODWIN, and ELIZABETH BROWN

1951 Evidence for a sex-linked lethal in the house mouse. Genetics, 36:235-53.

HOLLANDER, W. F., and L. C. STRONG

1950 Intra-uterine mortality and placental fusion in the mouse. Journ. Exper. Zool., 115:131-50.

LIU, T. T.

1953 The measurement of fertility and its use as an index of reproductive isolation among certain laboratory stocks of Peromyscus. Contrib. Lab. Vert. Biol. Univ. Mich., 59:1-12.

MAC DOWELL, EDWIN C.

1924 A method of determining the prenatal mortality in a given pregnancy of a mouse without affecting its subsequent reproduction. Anat. Rec., 27:329-36.

OSGOOD, W. H.

1909 Revision of the mice of the American genus Peromyscus. U. S. Dept. Agric., N. Amer. Fauna, 28:1-285.

SPUHLER, J. N.

1948 On the number of genes in man. Science, 108:279-80.

WATSON, M. L.

1942 Hybridization experiments between Peromyscus polionotus and Peromyscus maniculatus. Journ. Mammalogy, 23:315-16.

WHITE, M. J. D.

1945 Animal cytology and evolution London: Cambridge Univ. Press.

YERUSHALMY, G.

1939 Age of father and survival of offspring. Human Biol., 11:342-56.

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price, $0.45.

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN

Number 61 February, 1954

ARBOREAL ADAPTATIONS OF PEROMYSCUS, WITH SPECIAL REFERENCE TO USE OF THE TAIL*

By B. ELIZABETH HORNER

Accepted for publication September 18, 1952

CONTENTS

Introduction 1
Materials and Methods 3
Habitat and General Behavior 7
Climbing Behavior 13
Experiments 16
Discussion. 62
Summary 71
Literature Cited 72

INTRODUCTION

ADAPTIVE modifications, be they morphological, physiological, or psychological, are of universal importance in the animal world. The literature of zoology contains abundant evidence that animals show marked adaptation for a variety of habitats. Despite the vast literature on adaptations, however, few measurements have been recorded of their actual effectiveness in nature or in the laboratory.

The ecologic diversity of the various forms of mice of the wide-ranging genus Peromyscus has long been recognized. Some peromyscus live in swampy areas, some in prairie lands, some in arid desert lands, and others in forested areas. Concomitant with ecologic diversity in habitat many forms exhibit structural characters which may be presumed to be adaptive. This is particularly noticeable in regard to pelage color, which in peromyscus and many other small mammals tends to be positively correlated with the color of the surface soil (Dice and Blossom, 1937: 106-8; Dice, 1940: 213-15). That this like coloration is really protective has been demonstrated by experiments (Dice, 1947).

---

*A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

Contribution No. 228 from the Department of Zoology, Smith College.

With the exception of pelage color very little is known about the importance to peromyscus of characters which may be adaptive. Dice (1940: 215) suggested that the general correlation of tail length and hind-foot length with type of habitat may be essentially a correlation with habit; that is, the relatively longer tail and the relatively longer hind foot of the forest-dwelling forms, as compared with the prairie-dwelling, is possibly correlated with their semiarboreal habits. Since there has been too little information available to demonstrate such a positive correlation between body proportion and habit, the present study was largely designed to test this hypothesis.

The purpose of the investigation was threefold: (a) to study general arboreal performance in peromyscus, (b) to measure the arboreal behavior and ability of forms which in nature live in diverse types of habitat, and (c) to ascertain whether the long tail of a semiarboreal form is of greater aid to an arboreal life than is the short tail of forms which live in more open areas. The forms selected for study included five semiarboreal, four largely terrestrial, and one from a more or less intermediate habitat.

Although there are several references in the literature to climbing of peromyscus in nature, relevant experimental work in the genus is far more limited. Clark (1936) discovered certain consistent differences in geotropic behavior between very young mice of the semiarboreal and nonarboreal races he tested and Harris (1952) found that a terrestrial form and a semiarboreal form differed in their selection preferences for artificial habitats. The use of the tail as a balancing organ in house mice is described by Buck, Tolman, and Tolman (1925). Löhrl (1938) made laboratory observations of climbing ability in Apodemus, a genus of mice which appears to occupy some of the same ecologic niches in the Old World that members of Peromyscus do in the New. Apodemus sylvaticus, which reached its maximum density in a wooded-field habitat, was not, he found, demonstrably a less proficient climber than the generally longer-tailed, more exclusively forest-dwelling form A. flavicollis. A brief description of the use of the tail in climbing in Apodemus is also given by Löhrl (1938), based on the performance of captive mice trained to climb along small branches to obtain food. Dor (1937) studied the morphology of the caudal appendage as related to mammalian locomotion, and there are extensive works by Hatt (1932) and Howell (1932) which give an excellent survey of the use of the tail by ricochetal rodents. But all of this material, as well as that dealing with climbing in various nonperomyscan mammals, is related to the present problem in only a general way.

By reason of the paucity of specific information about climbing performance in peromyscus, the methods and apparatus used for testing in this study are largely original. It was necessary to devote much time to devising special techniques for measurement of climbing ability. The present report gives, therefore, only a partial survey of the scansorial adaptations within the genus.

Acknowledgments

This study was conducted under the direction of Lee R. Dice and the work performed at the Laboratory of Vertebrate Biology of the University of Michigan, which furnished the necessary facilities and materials for research. Financial assistance was provided by a University Fellowship and a Horace H. Rackham Predoctoral Fellowship, both awarded by the University of Michigan, and by the Sarah Watkins Wilder and Sarah Wheaton Whipple Fellowship of Smith College. The writer is also indebted to Smith College for the grant of a two-year leave of absence, from 1945 to 1947, during which time most of the experimental work was performed. The motion pictures were taken by Lee R. Dice with a camera loaned by the Cranbrook Institute of Science. Suggestions regarding the statistical treatment of data were offered by Charles W. Cotterman. Elizabeth Barto and William Jalosky assisted in the measurement of the living mice.

MATERIALS AND METHODS

Forms and Stocks

Five species, Peromyscus maniculatus, P. polionotus, P. leucopus, P. nasutus, and P. truei, are represented by the ten forms studied. A brief account of the collection of the original animals follows:

Peromyscus maniculatus bairdi (Prairie deermouse). -- Trapped by Merrel A. Taylor, in 1938, on the Todd Farm, near Fennville, Allegan County, Michigan.

Peromyscus maniculatus blandus (Chihuahua deermouse). -- Taken by W. Frank Blair, in 1938, near Tularosa, Otero County, New Mexico.

Peromyscus maniculatus gracilis (Forest deermouse). -- Trapped by W. Frank Blair, in 1940, at Pine Lake, Alger County, Michigan.

Peromyscus maniculatus nebrascensis (Sandhills deermouse). -- Trapped by Burton T. Ostenson and Palmer R. Sime, in 1935, near Kennedy, 40 miles south of Valentine, Cherry County, Nebraska.

Peromyscus maniculatus oreas (Cascades deermouse). -- Trapped by Lee R. Dice, in 1940, near Longmire, Mount Rainier National Park, Pierce County, Washington.

Peromyscus maniculatus rubidus (Redwood deermouse). -- Trapped by Lee R. Dice, in 1940, near Hood River, Hood River County, Oregon.

Peromyscus polionotus leucocephalus (Santa Rosa Island beach mouse). -- Trapped by W. Frank Blair, in 1942, on Santa Rosa Island, Santa Rosa County, Florida, opposite Camp Navarre, which is on the adjacent mainland.

Peromyscus leucopus noveboracensis (Wood mouse). -- Two stocks: one trapped by Ernest C. Driver, in 1943 and 1945, at Northampton, Hampshire County, Massachusetts; the other, by Lee R. Dice and B. Elizabeth Horner, in 1945, in Ann Arbor, Washtenaw County, Michigan.

Peromyscus nasutus nasutus (Juniper mouse). -- Taken by Lee R. Dice, in 1937, near Lincoln, Lincoln County, New Mexico.

Peromyscus truei truei (Pinyon mouse). -- Trapped by Lee R. Dice, in 1937, near Capitan, Lincoln County, New Mexico.

Inbreeding

Inbreeding of the stocks was kept at a minimum. Since all of them, however, except those of the form noveboracensis, had been in captivity for several years, a certain amount of inbreeding became imperative to maintain them. In spite of this, the body measurements of the mice used agree fairly well with those of the original animals of the several stocks. Although the animals available for study could not be expected to represent fully the respective wild populations, it is believed that they have provided reasonably valid measurements of the abilities and behavior characteristic of the natural populations.

Rearing and Handling

All recorded observations were made at the Laboratory of Vertebrate Biology of the University of Michigan, where the mice were maintained under essentially uniform conditions. The methods of rearing the mice varied only in minor details from those described by Dice (1929). The inverted aluminum nest pan, or "igloo" (Horner, 1947: 32), routinely placed in the cage of each mated female, was provided as a hiding place in many of the experiments.

Every effort was made to handle the mice gently and to accustom them to the presence of the observer. The cages were opened at frequent intervals and the nests cautiously examined. The mice were usually transferred from place to place, outside the cages, in glass water tumblers with the hand cupped over the open end. This method proved more satisfactory than the usual one of handling the mice with forceps, for it minimized the possibility of injuring their tails and produced less excitement in the captured animals. When it proved impracticable to induce a mouse to enter a tumbler, the animal was caught either in a live trap or in the cupped hands.

It was possible to tame the mice somewhat by conditioning them to a sound-food association. A sunflower seed was inserted through an opening in the wire mesh at the front of the cage and at the same time a squeaking sound was made. With few exceptions the mice quickly learned to respond to the auditory signal and readily took the seeds from the fingers. Sunflower seeds, highly prized by the mice, were never introduced into the food cup with the regular food supply, but were given only upon issue of the auditory signal or as rewards accompanying certain of the experiments.

In order to avoid foot injury a modification of the Laboratory method of individual identification, which utilizes toe cutting as well as ear punching (Dice, 1929: 122-23), was employed. For this study of climbing it was essential to limit the markings to ear punches. A system was devised employing both ears and only the ears. It ran up to 399 without duplication.

Body Measurements

In measuring the living, unanesthetized mice some modification of the usual method (Dice, 1932: 5-6) was required. Since measurements of live mice are likely to be less accurate than those of freshly killed animals, the body dimensions obtained are not strictly comparable with those obtained by the regular technique. The measurement of live, unanesthetized mice proved to be a two-person maneuver: the author made the measurements while another person held the mice. The modified procedure is given below.

Total length. -- Distance from tip of nose to tip of tail, not including the hairs. Mouse placed with its venter against a rule and stretched full length along it. Length recorded to the nearest millimeter.

Tail length. -- Distance from posterior limit of the two innominate bones to tip of tail, not including the hairs. Determined by pressing a specially designed rule against the skin covering the posterior faces of the bones. The rule had a small wooden block bolted on one end and set flush with the zero reading. The block was of such size as to make simultaneous contact with the two innominates without provoking excessive kicking. Length was recorded to the nearest millimeter. (Although the females of certain forms of peromyscus tend to have slightly longer innominates than do the males (Murie, 1933: 11-12), this fact is probably of little significance in the present study.)

Body length. -- Distance obtained by subtracting tail length from total length. Since tail length was slightly larger than when determined by the standard method, calculations of body length averaged somewhat smaller.

Hind-foot length. -- Distance from heel to tip of longest claw of left hind foot. Measured with a vernier caliper. Foot held straight between the thumb and index finger. Length recorded to nearest tenth of a millimeter.

Weight. -- Obtained by use of a laboratory balance. Recorded to nearest tenth of a gram.

Tail Amputation

Removal of the tail, a necessary part of several experiments, was accomplished by cutting across the tail, usually near its base, with sharp scissors which had been sterilized in 70 per cent alcohol. The severed part was measured to the nearest millimeter and the length of the stub calculated by subtracting the length of the detached portion from the original tail length.

Operations were of two kinds: (a) "half-tail" removal, in which the part removed equalled approximately one-half of the original tail and (b) "complete," in which a stub was left that was just visible as the mouse moved about. The length of the tail stub, measured from the posterior level of the innominates, averaged about 13 millimeters. All references, unless otherwise specified, are to complete tail removal.

Although most of the mice were anesthetized for the operation, no mouse was exposed to the ether fumes long enough to become more than partly inactive. This precaution was taken because at least one species of Peromyscus is particularly sensitive to ether fumes (Svihla, 1932: 14). Bleeding was slight. Amputees were placed immediately in clean cages, each mouse in a separate cage, and at least a month allowed before the animals were used. By that time the wounds had healed over completely.

Amputation of the tail appeared to have surprisingly little effect on the general behavior of the mice immediately following the operation. But their actions following release from their cages at the end of the convalescence period are of particular interest. When taken from their cages the animals were placed immediately on elevated platforms and forced to cross roughened glass tubes which they had learned to cross with considerable proficiency several weeks previously. The mice started across the tubes with no appreciably greater cautiousness nor appreciably less speed than shown immediately prior to the operation. Now considerably handicapped, they slipped more frequently and found it harder to right themselves when their hind feet slipped from the tubes. They appeared to be unaware of the cause of their difficulty in traveling upright and it was only after several slips that they began to travel more slowly and deliberately. This behavior, true to some extent of all of the mice, seemed to indicate that they were largely unaware of the loss of their tails. Possibly, life in the confined quarters of the small cages had made so few demands on tail use that the animals had either not become aware of the handicap or had so quickly learned to overcome it that they no longer recognized it. Certainly, their initial behavior on the climbing apparatus following tail amputation did not indicate noticeable awareness of the structural deficiency.

Experimental Rooms

Most of the experimental work was performed in two light-proofed reaction rooms in the Laboratory of Vertebrate Biology. Both rooms were provided with overhead lighting fixtures and wall switches, and the concrete floors were covered with a 1/2 - to 1-inch layer of sawdust.

The larger room measured approximately 9 by 21 feet, in inside dimensions, and was divided by a 2-foot-high, sheet-metal partition into two compartments, each approximately 9 by 10 1/2 feet. All corners were rounded by means of 2-foot-high, sheet-metal shields. Ventilation was provided by an electric fan, and passageways for the incoming and the outgoing air had light traps. There was a single door near one end, the opening guarded within by a 2-foot-high metal shield which prevented mice from escaping when the door was opened. The brick walls were heavily coated with smooth paint to a height of 2 feet to keep the mice from climbing them.

The smaller room measured approximately 7 by 8 feet, in inside dimensions, and its brick sides were painted to a height of 2 feet. There was a single door at the middle of one side, the opening provided with a smooth-painted wooden shield 18 inches high.

A few experiments were conducted in large metal drums located in a third room which was not light-proofed. Each drum was covered with a weighted wire-mesh lid which prevented escape of the mice and permitted adequate ventilation.

None of the rooms was soundproofed. There were only a few occasions, however, when experiments were discontinued temporarily because of excessive noise. Temperatures within the rooms varied approximately 30 degrees Fahrenheit over the period of study, but there was no indication that temperature differences affected in any way the experimental results.

HABITAT AND GENERAL BEHAVIOR

An extensive survey of the species of Peromyscus and their distribution over North America has been given by Osgood (1909). The brief descriptions given here are restricted to the ten forms covered by the present investigation. These accounts are concerned primarily with (a) the habitat preferences and terrestrio-arboreal habits and (b) the general behavior in captivity of the mice composing the stocks studied. Each of the ten forms studied differs somewhat in actions from each of the other forms. General behavioral characteristics, although frequently difficult of definition, affect in an important way the climbing activity of the mice and had to be taken into consideration not only in the evaluation of experimental results but also in the planning and conducting of the experiments. The descriptions of behavior are generalized and refer to the usual actions of the majority of individuals of the form. Within any form there will always be certain individuals which deviate considerably from the usual behavior pattern.

1. Peromyscus maniculatus bairdi. -- In various parts of its range inhabits prairie lands, open fields, and lake beaches, but everywhere seems to avoid forests (Dice, 1932: 4; Blair, 1940: 300-302). Largely terrestrial in habit, although Howard (1949: 12) reported that, under natural conditions, it occasionally climbs the bush clover (Lespedeza).

Bairdi mice tend to be timid and nervous. This is manifest in the relatively high frequency of hiding, trembling, chattering of teeth, cowering, and freezing when exposed to new surroundings. They explore cautiously and slowly at first and, even after they have become familiar with the new environment, perform very deliberately. They exhibit marked curiosity and considerable persistence in attempting difficult tasks.

2. Peromyscus maniculatus blandus. -- Occurs in habitats characterized by mesquite, creosote bush, atriplex, yucca, sumac, and other woody plants (Dice, 1930: 25; Blair, 1941: 225). Considered to be terrestrial in habit. No records are available to show that it climbs under natural, undisturbed conditions. Blandus, however, is actually capable of climbing the mesquite (W. F. Blair, personal communication), for an individual which escaped from one of Blair's traps, when chased, ran up into a mesquite bush and climbed about for several minutes before recapture. It is possible that the mouse could find no other retreat and behaved under stress quite contrary to normal. Even so, its behavior is obviously capable of modifiability.

Blandus mice are the least tractable of the ten forms. This conclusion does not agree with Svihla's (1932: 14), but it was the general opinion of workers in the Laboratory that the stock of blandus here described was very difficult to handle. These mice are nervous and highly excitable. When in strange surroundings they may remain perfectly motionless at the spot where placed or they may freeze, hide, run about in a rapid, jerky manner, or leap blindly in any direction. They were the least exploratory of the mice. Although fond of sunflower seeds, they rarely ate them during experiments of short duration.

3. Peromyscus maniculatus gracilis. -- Commonly associated with hardwood forest throughout its range. Although occasionally taken on lake beaches, in swampy regions, and in meadows, gracilis is seldom found any appreciable distance from forests (Dice and Sherman, 1922: 29-30; Dice, 1925a: 22-23; 1925b: 7) and is considered semiarboreal. Presumably, climbing plays an important role in the life of this form under natural conditions. Dice (1925b: 7) discovered three occupied nests under the rafters of a deserted dance pavilion. Johnson (1922: 37) captured an individual on the limb of a cedar tree about 4 feet from the ground. Van T. Harris (personal communication) recorded several instances in his field notes in which individuals climbed maple and beech trees when released from traps. Manville (1949: 32-33) noted their use of cavities in trees and stated that thirty-three climbed nearby trees when released from traps. One mouse ascended a hemlock about 30 feet before becoming lost to view. Among other trees climbed Manville mentioned oak, sugar maple, and basswood.

Gracilis mice are very tractable. Although they bite sharply and struggle vigorously when picked up, they become docile as soon as released. They explore new apparatus spontaneously and with apparent enthusiasm. Their movements are leisurely in contradistinction to the jerky movements of blandus or the more cautious, deliberate ones of bairdi. They exhibit marked curiosity and, even if they become momentarily excited, do not leap blindly from their positions.

4. Peromyscus maniculatus nebrascensis. -- Throughout its range limited fairly closely to sandhill country (Dice, 1941a: 1) characterized

by sparse vegetational covering. The vegetation is chiefly short grasses and yucca (B. T. Ostenson, personal communication), but a few shrubs, as sagebrush and rose, are present in parts of the range. Primarily terrestrial in habit. No records of climbing in nature are known to the writer and Ostenson (personal communication) found no evidence of it in the course of extensive field studies.

Nebrascensis mice are nervous and excitable but very curious and spontaneously exploratory. They sometimes freeze, or even jump blindly, when suddenly startled, but such behavior is usually followed almost immediately by a resumption of exploratory activity. These easily tamed mice showed so little fear of the observer's hands, often used to guide the mice toward a certain piece of apparatus, that they frequently climbed onto them and up her arms. This combination of fearlessness and curiosity made it difficult at times to direct the attention of the mice toward the desired object. On the floor they dug in the sawdust with relative frequency.

5. Peromyscus maniculatus oreas. -- Commonly associated with heavy coast forest characterized by such trees as Douglas fir, western hemlock, and red fir (Dice, 1949: 4, 22). Generally regarded as semiarboreal. Svihla (1933) found them inhabiting the dense underbrush of forests in the Olympic Peninsula of Washington. He recorded (1933: 13) an instance in which a mouse, upon escaping from a trap, ran rapidly to a nearby maple tree, and wrote: "I looked about hastily and accidentally glanced up into the tree. There, almost fifteen feet above me, was the mouse, climbing still higher with the ease and agility of a squirrel." Dalquest (1948) cited oreas as the only semiarboreal representative among six forms of Peromyscus occurring in Washington. He frequently caught oreas in traps set in trees for flying squirrels, and one individual was taken in a trap set 50 feet above ground.

Oreas mice behave in captivity very much like gracilis. The chief difference between them is that an oreas bites and struggles somewhat less when picked up and is even more leisurely and less excitable.

6. Peromyscus maniculatus rubidus (Hood River stock). -- Original mice of this stock trapped in cut-over land grown up to bushes and small trees, of which Douglas fir was dominant, a type of habitat intermediate between the heavily forested land which is the more usual home of rubidus and the adjacent areas of brushland inhabited by gambeli. A correlation of tail length with habitat among various stocks of rubidus was noted by Dice (1941b; 1949: 29). He found the tail of Hood River rubidus to be relatively shorter than that of several other stocks. Nothing is known to the writer regarding the role which climbing plays in the natural life of the Hood River rubidus, but presumably this brushland-inhabiting form is more or less intermediate in terrestrio-arboreal habits.

Rubidus mice, when held in the hand, struggle hard and sometimes bite, but they are not particularly excitable and constituted one of the more tractable of the forms.

7. Peromyscus polionotus leucocephalus. -- Occurring only on Santa Rosa Island, Florida, a beach-sand area. This is almost certainly

a strictly terrestrial form. No evidence of climbing has been reported for leucocephalus, although observations of its natural behavior have been made by several workers (Howell, 1920; Sumner, 1926; Hayne, 1950; Blair, 1951).

Leucocephalus mice are very excitable, jump readily upon occurrence of sudden sounds or movements, and are markedly hyperactive, moving rapidly from place to place in short, jerky runs. In spite of their excitability they can usually be trained without great difficulty by virtue of their spontaneous activity and very noticeable curiosity. They show marked persistence in repeatedly attempting difficult climbing feats. In their apparently fearless reaction toward the slow guiding movements of the observer's hands, they are somewhat like nebrascensis. Although many individuals climbed onto the hands, however, others took a more belligerent attitude. These mice boldly approached the hands and deliberately bit them or hit at them with one or both fore feet. This aggressive behavior was frequently accompanied by staccato squeaking. On the floor, like nebrascensis, they dug in the sawdust with relative frequency.

Along with the nervousness, or hyperactivity, of leucocephalus, and perhaps related to this activity, may be mentioned the relatively high frequency of face washing and the very noticeable cleanliness of the nests of this form. The nests are essentially hollow balls of cotton, and the cotton is kept clean and loosely fluffed out rather than being permitted to become matted down and soiled as is frequent with all of the other forms. It is interesting that the form which appears to be the most cleanly should also be the one to which marked personal cleanliness would presumably be most vitally important under natural conditions, for any concealing value which the predominantly white pelage of leucocephalus may have (Blair, 1951: 41) is dependent upon the continuous whiteness of that coat.

With reference again to the marked nervous activity of leucocephalus, it is possible that this activity, accompanied by the pronounced excitability of the form, plays an important role in escape from predators. A mouse running quickly in a straight line over an open expanse of sand could be overtaken readily by a more rapidly traveling predator. However, the tendency of leucocephalus to run rapidly in one direction for a short distance and then to turn suddenly and run in another direction, together with its tendency toward sudden leaping, might be expected, under certain circumstances, to confuse the predator to the extent of increasing the mouse's chances for survival. This same sort of zigzagging and sudden jumping is characteristic to a lesser extent of blandus and, to a still lesser extent, of nebrascensis, both of which inhabit relatively open country in many parts of their respective ranges.

8. Peromyscus leucopus noveboracensis. -- Occurs fairly generally throughout the hardwood forests of northeastern United States and eastern Canada and is almost entirely limited to wooded regions (Dice, 1937: 1; Burt, 1940: 16). Semiarboreal in habit. There is abundant evidence that they climb readily under natural conditions, and Nicholson (1941: 201-2) found, from a study of their use of nest boxes, that they actually prefer nest sites above the ground.

Although stocks from two widely separated parts of its range were used, the animals of both proved alike in behavior. Noveboracensis mice struggle very little and bite only rarely when picked up. They usually remain motionless and alert while being held and run or leap forward as soon as released. When pursued on the ground they run about in a rapid, excited manner. In running they tend to proceed directly from one landmark to another without pausing en route. When pursuit ceases they usually remain alertly motionless, ready to run forward at any moment. On elevated climbing equipment they generally remain motionless until urged into activity. Once aware of the part of the apparatus to be traversed, they perform unhesitatingly upon the slightest cue and by the most direct route available. Exploration of the apparatus is kept at a minimum.

9. Peromyscus nasutus nasutus. -- In the various parts of its range inhabits the yellow-pine association, the pinyon-juniper association, the rocky-slope association, or even the grassy-wash association (Dice, 1942: 205). It is found principally in regions characterized by rocks and brush or trees. The habitat is not limited to trees, but the mice seem to prefer them and are here classified as semiarboreal. Bailey (1931: 152), in describing the cliff-dwelling and tree-climbing habits of certain peromyscan mice of New Mexico, stated that the habits of nasutus are similar to those of P. boyli rowleyi. Since rowleyi is one of the most arboreal of all forms of peromyscus, Bailey apparently considered nasutus, likewise, to be somewhat arboreal under natural conditions.

Nasutus mice bite and struggle markedly when picked up, but are otherwise tractable. They explore leisurely and constitute one of the least excitable of the several forms. They are very much like oreas, for the most part, but are more curious and unlike them frequently resort to the apparently belligerent behavior of approaching, biting, and even hitting the observer's fingertips.

10. Peromyscus truei truei. -- Occurs most commonly in habitats containing such trees as yellow pine, pinyon, and juniper, although occasionally taken in grassland and certain desert regions (Dice, 1942: 205). Regarded as semiarboreal in habit. Their general type of habitat is similar to that of nasutus, and individuals of both forms are frequently taken in the same trap lines (Dice, 1942: 207). Observations of arboreal activity in truei were made by Bailey (1931: 152), who described their foraging activities not only along the bases of cliffs but also in the lower branches of nut-pine and juniper trees. He came upon one truei which lived in a nest of bark and sheep's wool located in the hollow trunk of a juniper tree. When not greatly disturbed, the mouse remained in its nest; but when alarmed, it climbed the smooth inside of the trunk with marked ease and agility. The type specimen was taken in a nest located 2 feet or more above the ground in the dead, hollow trunk of a small pinyon tree (Shufeldt, 1885: 403).

Truei mice usually struggle violently and bite sharply when picked up. They are markedly curious and spontaneously exploratory, and have, in general, little fear of slow, quiet movements of the observer. At times they are very tractable, at others, they behave in an excited manner, leaping suddenly and running rapidly. The excited activity of truei females with young has already been described by Svihla (1932: 14). Because of the unpredictability of the onset of excited activity, in individuals other than females with young, truei mice were particularly difficult to work with. Often they behaved very excitedly at first and, then, abruptly became fairly calm and docile. Sometimes the converse was true. Sometimes they failed to respond noticeably to strong stimuli, as the ringing of an alarm clock or a sudden movement; again they would respond markedly to weaker stimuli of similar nature. Sometimes the mice became suddenly excited for no apparent reason. Perhaps such unpredictable bursts of excitement in truei are correlated with special modifications of the sense organs. Possibly these mice are sensitive to a different range of stimuli than are the other forms of peromyscus studied.

Although no attempt to study modifications of the sense organs was made, the following observations suggest that certain modifications exist. Truei individuals upon several occasions went to the edge of an elevated platform and, with pinnae tensed, cocked their heads to listen to sounds made on the floor. Such individuals might listen to another mouse as it ran about on the floor or cracked the shell of a sunflower seed or might follow, as evidenced by head and ear movements, the observer's footsteps about the room. That a mouse was following the route of the observer by sound rather than sight was clear from the angle at which the head was held. This listening routine was manifested in its entirety only by truei, but members of other forms often executed certain phases of it. Truei seemed, too, to give overt response, either by ear twitching or other sudden change in behavior, to sounds of lower intensity than did the mice of the other forms. Whether a difference in auditory range or acuity actually existed is unknown, but truei was certainly keenly sensitive to sound and fairly good at localizing it. In this connection, the conspicuously large pinnae of this form are perhaps significant for, as Hoffmeister (1951: 34, 89-90) suggested, they may constitute an adaptation whereby truei, often living in regions where safe retreats are widely separated, may detect predators from afar and gain time in seeking refuge. Whether or not differences in vision exist among the various forms of peromyscus is also not known. The apparently larger size of the truei eye may be correlated with better vision, but observations of behavior made in the course of this study offer neither refutation nor support.

From the foregoing accounts it is apparent that most of the mice selected represented forms from two general types of natural habitat, terrestrial and semiarboreal, but one form came from a habitat of somewhat intermediate type. Those forms which live in nature in relatively open country are bairdi, blandus, nebrascensis, and leucocephalus, all of which are primarily terrestrial in habit as well as in habitat. Those which are semiarboreal both in habitat and habit are gracilis, oreas, noveboracensis, nasutus, and truei. The form which lives in brushland, a more or less intermediate habitat, is rubidus. Nothing is known about its terrestrio-arboreal habits. These ten forms represented five species. One of these species, maniculatus, included certain of the terrestrial (bairdi, blandus, nebrascensis) and semiarboreal (gracilis, oreas) forms as well as the form of intermediate habitat (rubidus).

In behavior the most tractable of the mice were the semiarboreal oreas, nasutus, and gracilis. Their behavior differed considerably from that of the other semiarboreal forms, noveboracensis and truei. Noveboracensis, ever tense and alert, gave the impression of performing in a direct, purposeful, and distinctly nonleisurely manner, whereas the enigmatic truei sometimes behaved in a most leisurely way and sometimes in a highly excited manner, its unpredictability at any given time being usually its most predictable characteristic. The intermediate rubidus, although less leisurely and exploratory than oreas, nasutus, and gracilis, was nevertheless tractable. The terrestrial forms showed various degrees of nervousness when exposed to new situations. Blandus, nebrascensis, and leucocephalus were especially excitable at such times. Nebrascensis lost its fear of new situations fairly readily; bairdi and leucocephalus lost theirs more slowly but then showed marked persistence in certain types of performance; and blandus was consistently least tractable. Additional characteristics of the mice studied included the marked cleanliness of leucocephalus and the digging tendencies of both nebrascensis and leucocephalus. All of the terrestrial forms did more digging than did any of the semiarboreal forms, but it was most frequently observed in these two forms.

CLIMBING BEHAVIOR

Use of Feet

In ascending tree trunks a peromyscus usually moves its feet one at a time, keeping three feet in contact with the trunk at any given instant (Pl. III, Q-T). Characteristically, the feet are moved forward in the following order: either fore foot, contralateral hind foot, ipselateral fore foot, contralateral hind foot. Although no records were kept of the number of instances in which the animals started forward with either the right foot or the left foot, there appeared to be no marked tendency to favor one side over the other in taking the first step. The feet, particularly the fore feet, are placed not directly under the body but somewhat to the side, the body remaining fairly close to the tree trunk. The main propulsive force seems to be exerted by the hind limbs, the fore limbs being used primarily in pulling the animal upward and then maintaining that forward motion. The toes are spread to some extent, and both the claws and the plantar tubercles are used in grasping the trunk. Although the feet are usually moved individually as the mice ascend trunks, in a few instances the animals moved their fore feet and their hind feet as pairs. A mouse ascending a trunk in this manner is shown in Plate III, U-X. This gait, which is more frequently observed among tree squirrels, was observed in a peromyscus only when the trunk climbed was one of relatively rough surface.

Descent of a tree trunk by a peromyscus is always head first (Pl. III, M-P). Both the feet and the toes are kept well separated. The mice tend to descend in an irregular spiral course, rather than directly downward. The spiraling is not shown in the figures, however, since, for photographic purposes, the mice were forced to descend the trunk along a narrow pathway. As descent is more difficult than ascent, the spiraling tends to distribute the weight of the mouse more at right angles to the line of gravitational pull and to reduce the tendency for the heavy posterior end of the body to roll outward and downward over the anterior end of the body. The oblique course also tends to reduce the degree of rotation required by the hind limbs in downward progression, so that more of the elongated plantar surfaces of the hind feet can be utilized to resist the downward pulling forces. In descent the feet are moved one at a time, three feet remaining in contact with the trunk as the fourth foot is moved to a new position. The maximum amount of rotation of the hind limbs seems to be about 120 degrees, whereas that observed in fox squirrels (Sciurus niger rufiventer) during the descent of tree trunks appears to be at least as great as 150 degrees.

In climbing along small branches the peromyscus usually keeps its toes spread well apart (Pls. IV, S; VI, A-L), although on very small branches the toes of the hind feet are sometimes held close together with their axes forming almost a right angle with the axis of the branch (Pl. IV, A-D). Both plantar surfaces and claws are used as the mice travel along the larger branches, but on branches of very small diameter the digital tips and claws often do not make contact with the branches. In sitting crosswise on a branch the mice usually keep the three middle toes of the hind feet fairly close together and spread the inner and outer toes of each hind foot. This manner of placing the toes is noticeable also when the mice travel more or less crosswise, as they occasionally do, along a branch of very small diameter or along a swaying branch of moderately small diameter.

The mice sometimes walk and sometimes run along horizontal branches. In progressing slowly the animals move their feet individually, keeping three feet in contact with the substratum at any given instant. The characteristic pattern of foot placement is illustrated in Plate VI, A-L. The order of raising the feet is as follows: either fore foot (left fore, A), contralateral hind foot (right hind, C and D), ipselateral fore foot (right fore, I), contralateral hind foot (left hind, L). As speed increases the mouse may continue to move its feet as described above (Pl. II, M-U), but with the occurrence of short intervals in which only two feet are simultaneously in contact with the substratum (Pl. II, M, N, Q). In traveling along a branch very rapidly, however, a mouse may break into a gait in which the hind feet are moved forward simultaneously, or almost so, and one fore foot is moved forward just before the hind feet strike the branch. In traveling rapidly along the ground or in running from a small branch onto a nearby support of considerable size, an animal may execute a half bound. In this type of gait the mouse raises its front feet, springs forward from its hind feet, and lands on first one fore foot and then the other, the first fore foot moving forward as the hind feet strike the substratum (Pl. II, B-K).

Use of Tail

In climbing peromyscus employs its tail as a prop, a balancing organ, a tactile organ, or a prehensile organ.

1. Prop. -- This use, in which the tail serves as a support, may be observed in a variety of situations. During ascent of a tree trunk a mouse usually holds its tail almost straight behind and close to the trunk. When ascent becomes arduous, the tail, pressed tightly against the trunk, helps to brace the weight of the animal. The proplike function of the tail is illustrated in Plate IV, U-V. Here the distal part of the tail is pressed against a projecting piece of bark, the animal having encountered (U) and then turned away from (V) a smooth-surfaced obstacle at the top of the trunk. In sitting crosswise on a small branch a mouse sometimes gains support by propping its tail against a nearby branch. On a fairly large branch an animal may employ its tail more or less like the third leg of a tripod, as it stands on its hind feet to wash its face or to investigate an overhanging object.

2. Balancing Organ. -- This use, in which the tail acts somewhat like the balancing pole of a tight-rope circus performer, is readily noted when a mouse travels along a flexible branch or along a nonflexible branch of moderately small diameter (Pls. III, B; IV, B-D). Under these conditions the mouse tends to keep its tail loosely flexed upward or behind, until balance becomes difficult; then the tail is tensed and waved conspicuously from side to side. As the weight of the mouse shifts too far to one side of the branch, the tail is waved toward the opposite side. If the entire tail is turned quickly to one side, movement of the posterior end of the body toward that same side may be rather sudden. If only the distal region of the tail is moved noticeably, movement of the hind quarters is considerably less abrupt. In general, the finer and more gradual shifts in balance are achieved by tail movements which do not appreciably involve the root of the tail. When balance becomes extremely difficult, however, the entire tail may be moved vigorously.

3. Tactile Organ. -- This use of the tail is particularly evident as a mouse travels about among small branches. The tail is waved gently behind in every direction. When it touches a branch, the tail is usually kept in contact with that branch, but not necessarily pressed against it or flexed over it, until the mouse has progressed so far forward that contact with it is lost. Should progression become difficult while the tail is in contact with a branch, the mouse will usually tighten the hold of its tail. Since employment of tail waving becomes more marked as locomotion becomes more difficult, the tail is most likely to encounter accessible branches at times when they can serve most effectively as an aid to locomotion (Pl. VII, U-X).

4. Prehensile Organ. -- A fourth function of the tail in scansorial activity is that of prehensility. No mouse was observed to hang by its tail, but as it travels along a hazardous pathway, flexing the tail over a nearby object enables the animal to brace itself somewhat as it seeks a secure foothold. In descending from one branch to another, a mouse can place its fore feet on the lower branch and then drop its hind feet toward the

same support while still maintaining its hold on the upper branch by means of the flexed tail (Pls. III, G-H; V, C-F, L-R; VII, G-K). The hold of the tail on the upper branch diminishes the rate of descent of the relatively heavy posterior part of the body and gives the animal more time to place its hind feet accurately below. When a mouse slips to the underside of a branch on which it is traveling, it almost always flexes its tail around that branch (Pls. III, D-F; IV, G-H). The flexed tail then helps to support the weight of the mouse as it clings to the underside of the branch and the tail may also serve to brace the animal in attempts to regain an upright position (Pl. IV, H; VI, M). In such an attempt, the flexing of only the distal region of the tail over the branch by the mouse permits the hind quarters greater freedom in making the appropriate righting movements.

EXPERIMENTS

I. Inclination to Climb

This experiment was designed to determine whether any of the forms of mice under study exhibited a natural aversion to climbing. The mice were offered an apparatus that all of them could climb easily and were given time to explore it freely. That the apparatus was actually well within the climbing ability of the mice was determined by preliminary observations of several extraexperimental representatives of each of the stocks studied, as well as by postexperimental observations in which individuals which did not climb during the experiment were found to climb the same apparatus readily when it afforded the only means of escaping from an area of confinement.

The apparatus (Pl. I, A) consisted of four elevated runways set at a height of 21 inches above four ground-level runways. The runways of each level radiated at right angles from a central support. The support was constructed of wood and provided with lath steps of such roughness and arrangement that any of the mice could easily climb to the top. The lower runways were roofed over with three-eighths-inch-mesh wire screen in such a manner that entrance to any runway could be gained only from the end adjacent to the central support. This made entrance to the lower runways comparable to that to the upper, there being only a single place of entrance to any runway and that next to the central support of the apparatus. Consequently, any mouse which explored a lower runway was necessarily made aware of the presence of the support which led upward, and no mouse which explored a lower runway could avoid the upper runways merely because random movements about the room did not lead it to the central support. All runways had metal sides and ends and were filled in with sand. The presence of tracks in the sand indicated the extent of exploration along the runways. The entire apparatus was placed on a flat baseboard which prevented in large measure the tracking into the runways of the sawdust covering the rest of the floor. Food, water, nesting material, and cover were all available in the vicinity of the apparatus in the middle of the room.

The number of mice tested was 80, 8 of each form. The sexes were equally divided. The mice were tested singly in a definite order as to stock and sex (the so-called "pairing method" of statistical usage). Each mouse was placed in the reaction room overnight and allowed free exploration. Since peromyscus is mostly nocturnal even in captivity (Johnson, 1926; Behney, 1936; Whitaker, 1940), each mouse was tested in total darkness -- the optimum condition for activity in blandus (Blair, 1943) and presumably for other forms of peromyscus as well. At the end of a test period the mouse was removed, its activity recorded, the sand smoothed over, and the food and water replenished. Each mouse remained in the reaction room approximately 24 hours.

TABLE I

Peromyscus Exploring Runways at Each of Two Levels of Elevation

Species and Subspecies	Number of Mice Tested	Number of Mice which Explored One or More Runways at Ground Level	Number of Mice which Explored One or More Runways at Upper Level
Terrestrial:			
maniculatus bairdi	8	8	8
maniculatus blandus	8	8	5
maniculatus nebrascensis	8	8	7
polionotus leucocephalus .	8	8	7
Intermediate:			
maniculatus rubidus	8	8	8
Semiarboreal:			
maniculatus gracilis	8	8	7
maniculatus oreas	8	8	8
leucopus noveboracensis .	8	8	8
nasutus nasutus	8	8	8
truei truei..............	8	6	7
Total	80	78	73

The great majority of the mice explored at least one runway at each level of the apparatus (Table I). Of the 80 mice tested only two individuals, both belonging to the semiarboreal form truei, climbed to the runways of the upper level without exploring the lower level. Three blandus, one gracilis, one nebrascensis, one leucocephalus, and one truei failed to explore the upper level.

The difference between the total number of mice which explored at ground level and the total number which explored at the upper level was not statistically significant (chi-square equals 0.17, with 1 degree of freedom). The greatest difference within any one form in regard to exploration at both levels was shown by blandus, of which eight individuals explored at the ground level but only five climbed to the upper level. Here the chi-square value for the difference is 0.69, which still falls well above the 5 per cent level of probability. At neither level of the apparatus was absence of exploration correlated with either age or sex. Records kept of the number of mice exploring each individual runway at the two levels indicate that there were no directional preferences for any particular runway and that exploration of the several runways at a given level was at random.

The results of this experiment show that none of the ten forms of peromyscus tested were averse to climbing when the apparatus to be climbed was sufficiently easy and the mice were allowed to explore it freely. A few individuals, for reasons unknown, did not explore the apparatus at either one level or the other.

II. Reaction to High Places

In this experiment measurements were obtained of the reactions to high places of the ten forms under study. Reaction of mice to high places is an important factor in their climbing behavior, because such attributes as awareness of height, judgment of distance between branches, and fear of falling are involved.

The studies were conducted in the large reaction room. One compartment served as the experimental room proper and the other as an observation room. The two compartments were completely separated by a dark burlap curtain. The curtain was made into an effective one-way-vision screen by inserting an observation window of white cheesecloth in the center. The side of the burlap facing the experimental compartment was coated with white paint, and the cheesecloth facing the observation compartment was streaked with black paint to camouflage the outlines of the observer behind the screen. The experiment took place under dim light. During the early stages a 10-watt frosted bulb was used in the ceiling fixture of each compartment. That in the experimental compartment was later replaced by one of 15 watts because of difficulty in observing certain movements of the mice.

In the center of the experimental compartment was located a round elevated platform supported by a single metal rod. The platform measured 14 inches in diameter and its upper surface was 27 inches above the floor. A small, bottomless, wire-sided cage lined with transparent plastic sheeting was centered on the platform and a single sunflower seed placed under it. The roof of the cage was constructed of smoothly finished wood and was essentially a hinged door which could be readily locked when closed. With the door locked the entire cage could be lifted free from the platform (Pl. I, B) by means of a pulley mechanism operated from the observation compartment.

Testing procedure was as follows. Each mouse was removed from its own cage and transferred to the cage on the platform. The observer took up a position behind the curtain and set an interval timer for a seven-minute period. After two minutes, to give the mouse opportunity to become somewhat oriented to its new surroundings, the cage was raised to a specified distance (approximately 4 feet). The smooth transparent lining prevented the mouse from clinging to the sides of the cage and permitted observation of prior activity. As soon as the cage was raised the mouse was free to move about on the open elevated platform. The behavior of the unconfined animal was observed for five minutes, the length of the actual test. The mice were tested, insofar as practicable, in the same general order as in Experiment I. Ages varied considerably within each form and in some of the forms ranged from six weeks to three years. No correlation of age, or of sex, with any tested type of behavior was found.

TABLE II

Reaction of Peromyscus to Elevation on Open Platform

Mice permitted to explore freely for a five-minute test period.

Species and Subspecies	Number of Mice Tested	Number Remaining on Platform for Five Minutes	Percentage Remaining on Platform for Five Minutes
Terrestrial:			
maniculatus bairdi	17	10	59
maniculatus blandus	18	9	50
maniculatus nebrascensis ..	14	5	36
polionotus leucocephalus ...	14	5	36
Intermediate:			
maniculatus rubidus	12	8	67
Semiarboreal:			
maniculatus gracilis.......	18	15	83
maniculatus oreas.........	10	9	90
leucopus noveboracensis ...	10	10	100
nasutus nasutus	10	9	90
truei truei................	16	8	50
Total	139	88	

The reactions of the mice to elevation on an open platform are given in Table II. The number (88) of mice which remained on the platform for five minutes is significantly greater than the number (51) which left it (chi-square for the difference equals 9.85, with 1 degree of freedom). The forms with the highest percentages of individuals remaining on the platform for the full test period were the semiarboreal noveboracensis, nasutus, oreas, and gracilis, and the lowest were the terrestrial leucocephalus and nebrascensis. Intermediate were the semiarboreal truei, the terrestrial blandus and bairdi, and the transitional rubidus.

Far more individuals of the semiarboreal forms, as a group, than of the terrestrial forms, as a group, remained on the platform for the five-minute period. Of the total number of individuals (64) in the semiarboreal group (18 gracilis, 10 oreas, 16 truei, 10 nasutus, and 10 noveboracensis), 51 stayed on the platform, whereas of the total (63) in the terrestrial group (14 leucocephalus, 14 nebrascensis, 18 blandus, and 17 bairdi), only 29 remained for the full period. The difference between these two groups in the relative numbers of mice remaining is highly significant statistically (chi-square equals 15.43, with 1 degree of freedom). Because of its intermediate natural habitat rubidus was not included in either the terrestrial or the semiarboreal category.

That the average length of time which the mice remained on the platform would have been much shorter had it been closer to the ground was demonstrated by the behavior of a control group. This group of 45 animals, representing all of the forms except noveboracensis, was tested under the same conditions previously described except that the platform was now located only an inch above the floor. Since no noveboracensis were available for controls, noveboracensis were not used in calculating the average time spent on the elevated platform by the semiarboreal mice. No member of the control group remained on the low platform for the full five minutes and the average time at which these mice left the platform was 0.51 minutes after the cage was raised. The average time which the controls remained on the platform was 0.64 minutes for the 22 terrestrial individuals and 0.37 minutes for the 19 semiarboreal ones. The average time spent on the elevated platform, on the other hand, was 3.10 minutes for the 63 terrestrial mice and 4.18 minutes for the 54 semiarboreal individuals. Since the terrestrial controls remained on the low platform longer, on the average, than did the semiarboreal, there seems to be no doubt that the tendency of the mice of the semiarboreal forms to remain longer on the open elevated platform than those of the terrestrial forms was due primarily to the greater elevation.

The data thus far presented show that in the absence of pathways to the ground semiarboreal mice are much more likely than terrestrial ones to remain on an elevated apparatus. The reaction to high places cannot, however, be regarded as a simple response, for the mice which left the elevated platform appeared to do so for diverse reasons. An analysis of their methods of reaching the ground is considered under four general categories: (1) running over the edge of the platform without giving evidence of previous awareness of the edge; (2) falling over the edge but evidently aware of its presence; (3) dropping from the edge deliberately; and (4) jumping from the edge deliberately. The proportion of mice using each method is given in Table III.

1. Running over Edge. -- Seven of the 139 mice tested ran off the platform almost immediately after the cage was raised without giving evidence of being aware of the presence of the edge. The action appeared accidental rather than deliberate, but was probably influenced by their excited state. Whether or not excitement was the main cause, however, is problematical, for some mice, particularly noveboracensis, although apparently highly excited, controlled their running in time to keep from

going headlong over the edge. Perhaps certain of the mice, despite a state of great excitement, were more alert to stimuli in the external environment than others which were equally excited. There is also the possibility that some individuals which appeared to be greatly excited were actually not so much so as others outwardly more calm.

There is no significant evidence that the excited behavior exhibited by the mice which ran over the edge was caused by their awareness of the elevated position. In the control group none of the 45 mice tested left the one-inch-high platform without first pausing at the edge and thereby giving evidence of awareness of the edge. That seven of the 139 individuals tested on the elevated platform ran off without any attempt at exploration or any noticeable previous awareness of the edge, whereas none of the 45 controls behaved similarly, may have been due to chance alone. The adjusted chi-square value for comparison of the difference between the number of mice running off the platform and the number not running off in the two tests is 1.18, with 1 degree of freedom. The adjustment used is that of Yates.

TABLE III

Methods of Reaching the Ground Employed by Peromyscus Which did Not Remain on Open, Elevated Platform for Full Five-minute Test Period

Species and Subspecies	Number of Mice which Ran off Platform	Number of Mice which Fell off Platform	Number of Mice which Dropped off Platform	Number of Mice which Jumped off Platform
Terrestrial:				
maniculatus bairdi	1	5	1	0
maniculatus blandus	2	7	0	0
maniculatus nebrascensis	0	8	1	0
polionotus leucocephalus .	2	6	1	0
Intermediate:				
maniculatus rubidus	1	1	0	2
Semiarboreal:				
maniculatus gracilis.....	0	2	1	0
maniculatus oreas.......	0	0	1	0
nasutus nasutus	0	1	0	0
truei truei..............	1	0	2	5
Total	7	30	7	7

Of the 139 mice, 1 of the 12 rubidus, 5 of the 63 terrestrial, and 1 of the 64 semiarboreal mice ran off the elevated platform during the five-minute test period (Table III). The adjusted chi-square value for the difference between the number of mice running off and the number not running off in the terrestrial and the semiarboreal groups is 1.62, which is not significant.

2. Falling over Edge. -- All of the 30 mice which reached the floor by falling off the platform appeared to do so accidentally rather than deliberately. Their behavior indicated that they recognized the presence of the edge of the platform, yet they slipped over despite this awareness. Several struggled hard to recover their lost footings, but fell anyway. A few seemed to lose their footholds at the edge as a result of rapid or jerky exploration. Many walked over the edge for no apparent reason whatsoever. Although two or three of the mice showed excitement, the animals which fell were not, as a whole, particularly excited. The characteristic which best distinguished those that fell, as a group, was their relative lack of exploration of what lay beyond the edge of the platform. Most of the mice explored to the extent of bringing the tips of their noses close to the edge, then failed to go close enough to look over it to the floor below. Whatever the reason for the low frequency of exploration, the mice probably would have been less likely to slip over the edge had they become more fully aware of its relationship to the ground. Another factor which seemed partly responsible for the falling of a few mice was clumsiness, but this may have been, at least to some extent, a manifestation of nervousness.

Among the mice which fell off there were far more representatives of terrestrial than semiarboreal forms. Twenty-six of the 63 terrestrial individuals tested fell over the edge, but only 3 of the 64 semiarboreal animals had that misfortune. One of the 12 rubidus also fell over the edge. Comparison of the terrestrial and the semiarboreal groups with respect to total numbers of individuals falling and not falling during the five-minute test period gives an adjusted chi-square value of 22.08, with 1 degree of freedom, which is highly significant. The semiarboreal mice are, therefore, shown to be far less likely than the terrestrial mice to fall off the elevated platform.

3. Dropping from Edge. -- All of the mice which dropped to the floor appeared to do so deliberately, as though well aware of the elevated position but anxious to leave the platform. In dropping the animals let themselves gradually over the edge until their heads and fore limbs hung free from the platform and only the plantar surfaces of their hind feet gripped the upper surface of the platform. Their tails were sometimes held in contact with the upper surface of the platform, but not always. The footwork required considerable rotation at the ankle joint as well as at the knee and hip joints. The rotation exhibited appeared to be similar, but perhaps less in degree, to that observed in squirrels descending tree trunks.

The mice appeared to recognize the general relationship of the platform to the floor. The majority in the course of exploration of the edge extended their heads well over it and looked down toward the ground; most of them recovered from at least one hind-foot hold before finally dropping. As a group they seemed excited but fairly cautious. Dropping in the described manner provided a method whereby the mice could get as close as possible to the floor before releasing their holds on the edge of the platform.

Of the mice which dropped to the floor three were terrestrial and four semiarboreal. The difference between the numbers of mice dropping and not dropping in the two groups gives an adjusted chi-square value of 0.0005, which is not significant.

4. Jumping from Edge. -- The seven mice which jumped to the floor seemed more excited than the mice which dropped. All individuals which jumped did so within a minute of the time the cage was raised and all appeared to jump deliberately. Although they explored very little before jumping, all of them paused at the edge and looked well over it toward the floor before leaving the platform. Jumping was always from the edge of the platform and the animals landed on the floor usually 2 to 4 feet from the base of the platform support. Their powerful jumps indicated that they recognized the platform to be well above the level of the floor.

Five of the mice which jumped belonged to the semiarboreal truei and two to the transitional form rubidus. Comparison of the terrestrial and semiarboreal groups with regard to numbers of mice jumping and not jumping gives an adjusted chi-square of 3.27, with 1 degree of freedom, which is not significant.

It seems particularly noteworthy, however, that the majority of the semiarboreal mice which left the platform during Experiment II did so deliberately, either by jumping or by dropping from the edge, and with awareness of the general relationship of the platform to the floor; whereas the majority of the terrestrial individuals left it accidentally, either by falling or by running from the edge, and with far less awareness of the elevation from the floor. Comparison of the semiarboreal and terrestrial groups with regard to numbers of individuals leaving the platform deliberately and those leaving it by accident gives an adjusted chi-square value of 15.01, which is highly significant.

Evidence that mice of the genus Peromyscus have an innate fear of falling is given by the large number (88) of mice remaining on the elevated platform for the full five-minute period, by the several recoveries attempted by mice which slipped accidentally over the edge, and by the many mice which took precautions toward making a safe landing before leaving the platform. Approximately half of the mice, furthermore, had never before been exposed to free exploration at any elevation greater than approximately 6 inches; yet the reaction to the elevated position of these mice, which had spent all of their lives in cages, differed in no apparent manner from that of the mice which had previously experienced considerably elevated positions. The dependency of an innate fear of falling upon the efficiency of the sensory mechanisms is known. In the terrestrial forms this fear seems to be less well-developed than in the semiarboreal and these forms may prove to be less sensitive to certain of the stimuli involved in the recognition of elevated position.

The results of this experiment show that mice of the forms tested differ in reaction to high places. The semiarboreal forms, gracilis, oreas, nasutus, truei, and noveboracensis, as a group, had a significantly greater tendency to remain on an elevated platform for the duration of a five-minute test period (79.7 per cent of the mice remained) than did the terrestrial forms, bairdi, blandus, nebrascensis, and leucocephalus, as a group (46.0 per cent remained). Rubidus, intermediate in habitat, was more or less intermediate between the semiarboreal and the terrestrial forms in reaction to elevation (66.7 per cent remained). The terrestrial mice were significantly more likely to fall from the platform than were the semiarboreal mice. Most of the semiarboreal individuals which left the platform during the test period seemed to do so intentionally, and they appeared to be well aware of the general relationship of the platform to the ground. On the contrary, most of the terrestrial mice which left the platform seemed to do so accidentally and with less awareness of the elevation. The experiment gives fairly good evidence that the mice tested have an innate fear of falling.

III. Climbing Vertically

The following three experiments were designed to test the ability of the mice to ascend upright objects.

1. Climbing Tree Trunks. -- In the first of these experiments selected sections of natural trunks were employed to ascertain the ability of the mice to climb trees of various kinds and sizes. The trunks were placed in the reaction room containing the two-level runway apparatus and the experiment conducted concomitantly with Experiment I. The number of trunks climbed as well as the number of runways explored were both recorded at the end of each test period. The tree trunks which were employed were those of Ailanthus glandulosa (tree of heaven), Fagus grandifolia (beech), Gleditsia triacanthos (honey locust), Acer negundo (box elder), and Ulmus americana (elm). Their heights and diameters are given in Table IV. The diameters were derived from circumference measurements taken 5 inches from the base, although each trunk was fairly uniform throughout its height. All trunks retained their natural coverings of bark throughout the experiment. The top of each section was completely covered with a layer of sand held in place by a peripheral ring of putty. Tracks in the sand were taken as indication that the mice had climbed to the top. Other conditions of the experiment have been described under Experiment I.

Mice of all the forms climbed a majority of the trunks offered (Table IV). The terrestrial blandus climbed the least total number of trunks (26) and the semiarboreal noveboracensis climbed the greatest (46). The total trunks climbed by blandus was significantly less than that climbed by either noveboracensis (chi-square equals 5.55, with 1 degree of freedom) or oreas (chi-square equals 4.19, with 1 degree of freedom), both semiarboreal forms. These were the only statistically significant comparisons obtained. The next greatest difference was that between the scores of blandus and truei, which gives a chi-square value of only 3.39.

A large majority of the mice climbed each of the following trunks: Ailanthus, Gleditsia, Acer, and Ulmus. All these were climbed in almost equal numbers by the mice, and the greater height of one of the two Ailanthus trunks proved no discouragement.

Mice of all of the forms showed a certain, some a very marked, degree

TABLE IV

Peromyscus Which Ascended Tree Trunks

Measurements of trunks recorded to nearest half inch.

Species and Subspecies	Number of Mice Tested	Number of Mice Which Climbed Each Kind of Trunk						Total Trunks Climbed
		Ailanthus (ht. 1'2"; diam. 9")	Ailanthus (ht. 3'½"; diam. 9")	Fagus (ht. 1'7½"; diam. 3")	Gleditsia (ht. 1'7"; diam. 5½")	Acer (ht. 3'10½"; diam. 10")	Ulmus (ht. 3'6½"; diam. 10½")	
Terrestrial:								
maniculatus bairdi	8	8	7	4	7	7	7	40
maniculatus blandus	8	5	4	0	5	6	6	26
maniculatus nebrascensis	8	8	8	2	7	8	7	40
polionotus leucocephalus .	8	7	8	0	7	8	8	38
Intermediate:								
maniculatus rubidus	8	7	7	3	7	7	7	38
Semiarboreal:								
maniculatus gracilis.....	8	7	7	4	7	7	7	39
maniculatus oreas........	8	8	8	4	7	8	8	43
leucopus noveboracensis .	8	8	8	6	8	8	8	46
nasutus nasutus	8	6	7	3	7	8	7	38
truei truei.............	8	8	8	1	8	8	8	41
Total Mice which climbed each trunk		72	72	27	70	75	73	

of discrimination against the Fagus trunk. But, with the exception of blandus and leucocephalus, which are both terrestrial under natural conditions, all of the forms had at least one representative which climbed it. The form with the greatest number of representatives climbing the Fagus was the semiarboreal noveboracensis; six of these mice achieved such success. Comparison of the terrestrial forms, bairdi, blandus, nebrascensis, and leucocephalus, as a group, with the semiarboreal forms, gracilis, oreas, noveboracensis, nasutus, and truei, as a group, with regard to the relative number of mice which climbed the Fagus, gave an adjusted chi-square value of 6.76, with 1 degree of freedom; that is, significantly more semiarboreal than terrestrial mice climbed this trunk. Comparable chi-square values obtained by comparing rubidus with the terrestrial and the semiarboreal groups are 2.59 and 0.00, respectively, neither of the values indicating significance.

Of the 80 mice tested (8 from each of the 10 forms) only 27 climbed the Fagus, whereas at least 70 mice climbed each of the other trunks offered. In addition to the results given (Table IV), observation made clear that the smooth-, hard-barked trunk of Fagus was more difficult for mice of all of the forms to climb than were the rough-barked (Acer, Ulmus) or the soft-barked (Ailanthus, Gleditsia) trunks. That discrimination against Fagus was actually due to a difficulty in climbing rather than some other factor, such as odor, was confirmed many times. Moreover, none of the mice exhibited difficulty in climbing any of the other trunks listed (Table IV). Several times mice were seen struggling to to climb the Fagus. They reached well up onto the trunk with their fore feet, as though trying to get a firm hold on the bark; then, if they did not almost immediately give up the ascent apparently intended, they sometimes obtained a hold with one hind foot, only to fall back to the ground when attempting to place the other hind foot on the trunk. Frequently, a mouse would manage to grasp the trunk with all four feet, but would fall almost immediately in attempting to climb farther. That some of the mice were able to climb the Fagus more easily, however, was confirmed by observation as well as by the record.

As seen from Experiment I, all of the forms of mice tested had a natural tendency to climb, if an object presented was sufficiently easy and they were given ample time to explore freely. In the present experiment the Fagus trunk was the only one presented which proved markedly difficult for them. If Fagus is eliminated from the data of Table IV, there are no significant differences in the total numbers of trunks climbed by any of the several forms of mice. Again, the terrestrial blandus exhibits the lowest total climbing score (26 trunks climbed), but the difference between its score and the maximum score (40) attained by both truei and noveboracensis falls short of statistical significance (chi-square equals 2.97).

Supplemental material on trunk climbing was obtained by using trunks of two additional kinds. One was the hard-, rough-barked trunk of Prunus aucuparia (apricot). The section measured 14 inches in height and 4 1/2 in diameter. The Prunus trunk was added to the others in the experimental room for 10 successive 24-hour periods, while 10 mice, including a representative of each form, were tested. All of these individuals climbed the Prunus and all other trunks present except the Fagus, which was climbed by only two of them. The mice, therefore, were well able to climb the rough-barked Prunus despite the hardness of its bark.

Another trunk, introduced later, was from a tree of unknown genus. It was smoother than, but not quite so hard as, the Fagus. The section used measured 20 inches in height and 1 1/2 inches in diameter. It was left in the experimental room for 20 nights while two individuals of each form were tested. During the 20 test periods the mice showed noticeable discrimination against only two of the trunks, that of Fagus and that of unknown name. Of the 20 mice, 8 climbed Fagus, 7 climbed the unidentified trunk, and at least 14 climbed each of the other trunks. Of the mice which climbed the unidentified trunk there were two terrestrial and four semiarboreal , but the difference in the relative numbers of terrestrial and semiarboreal mice which climbed this trunk is not of statistical significance (chi-square equals 1.38). The results do suggest, however, that both smoothness and hardness of bark are factors which limit the trunk-climbing ability of the mice. A third factor which might be considered important is smaller diameter, but this was ruled out by evidence to be presented below (Experiment III, 2).

Observations of mice climbing the unidentified trunk were far fewer than for the Fagus, but in a few instances individuals were seen experiencing difficulty in climbing, or attempting in vain to climb, this trunk. The bark of this trunk, although a little softer than that of Fagus, was sufficiently hard to prevent ready penetration by the claws of the mice, and its excessive smoothness apparently offered a minimum of friction surface for effective grasping of the trunk by both the foot pads and the claws.

The results of this experiment show that all the peromyscus studied were well able to climb vertical trunks covered with bark which is either markedly rough (Acer, Ulmus, Prunus) or slightly rough and moderately soft (Ailanthus, Gleditsia), but that all of the mice had difficulty with trunks on which the bark was either very hard and only slightly rough (Fagus) or very smooth and fairly hard (unknown species). Furthermore, although all experienced difficulty in climbing the Fagus trunk, the semiarboreal mice experienced significantly less difficulty than did the terrestrial mice.

2. Climbing Tubes of Uniform Roughness but Progressively Greater Diameter. -- The second experiment of this group was designed to measure the comparative ability of the mice of the 10 forms to climb vertically on tubes of a given degree of roughness but which differed from one another in progressively greater diameter. Results of several preliminary tests indicated that, given tubes of uniform roughness, those of large diameter were more difficult for the animals to climb than those of small diameter; also, the tests showed that some individuals experienced greater difficulty than others.

Advantage was taken of the fact that the mice, when confined to small quarters devoid of hiding places, usually attempted to escape by any means at hand. In this experiment a tall glass cylinder of large diameter constituted the area of confinement and a vertical, axially located, roughened 2-foot glass tube the means of escape. Each mouse was trained for the experiment (see below) and the reward offered was escape from the narrow confines of the cylinder, with its lack of hiding places, to more roomy quarters outside, where a protective nest pan and an abundance of nesting material were available. Across the open top of the cylinder was placed a landing platform. The climbing mice were able to reach the platform easily from the vertical tube and could then travel down a gradually sloping pathway to the ground.

The eight tubes presented the mice were of the following outside diameters: 7.0, 19.3, 25.1, 30.0, 35.6, 40.0, 44.5, and 49.7 mm. A ninth tube of 63.4 mm. was also offered for a considerable period, but, since no mouse ever climbed it, its use was finally discontinued. The uniform degree of roughness of the outsides was furnished by covering the tubes evenly with 600-mesh Crystolon, a silicon carbide abrasive material ground to that size. Each tube was coated with brushing lacquer and then rolled immediately in the Crystolon. The covering was not only uniform but remarkably resistant to wear. Tubes were replaced whenever a surface became marred by feces.

Each tube was supported from within by a sturdy vertical support, secured to a horizontal baseboard, which centered the tube within the cylinder or jar. A tube could be readily slipped over the support and placed in proper position. The upper ends of the larger tubes were provided with corks to prevent the mice, when they climbed to the top, from falling into the tubes. In each jar was placed a 24-hour supply of food and water and sufficient cotton batting to enable a mouse to keep warm, but not enough to constitute a hiding place. A shallow layer of sawdust in the bottom of the cylinder served as a moisture absorbent. The space outside the jar was always larger than that within it and contained the standard food, with the addition of sunflower seeds, and a nest pan with sufficient cotton batting for a nest.

The 10 cylinders used ranged in height from 20 to 31 inches. In inside diameter they were approximately 8 1/2 to 11 1/2 inches. Four of the cylinders were made taller than the standard 20- and 24- inch heights by inserting linings of plastic sheeting which continued upward beyond the original tops. The tallest cylinders were resorted to in cases where jumping rather than climbing from a jar was suspected.

The experiment was conducted and scored as follows. A mouse was placed in a cylinder containing a vertical tree trunk of small diameter and of such roughness that any of the mice could easily climb it. Once a mouse had climbed from the cylinder and explored the space outside, the smallest tube in the series, the 7.0 mm., was substituted for the trunk and the mouse again placed in the cylinder. When the mouse had escaped by way of this tube, the next larger tube in the series, the 19.3 mm., was inserted and the mouse put back. This was repeated until the mouse, after a period of 24 consecutive hours, had still not escaped from the cylinder. Whichever tube was then in the jar was replaced by the tube next smaller to it, the food and water replenished, and the mouse closely observed. If it climbed the smaller tube, the next larger one, previously rejected, was returned and the mouse in due time was returned to the cylinder. If the animal again failed to climb the larger tube while being observed, but was absent from the cylinder later on, it was once more returned to the cylinder. It was always considered necessary to see the mouse in the act of climbing the critical tube in the series before scoring it as having done so, and it was also necessary to witness any futile attempts to climb the next larger tube in the series. No mouse was scored as having climbed a given tube unless it had climbed at least a foot upward along it. This distance was not accurately determined, however, until the limit of the climbing ability of the mouse was approached. Individual records kept for each mouse indicated the order in which the tubes were presented, the tubes apparently climbed, the tubes actually observed to have been climbed, and the tubes attempted in vain. The maximum number of different-diametered tubes which an animal was able to climb, as determined by direct observation with regard to the critical tube, represented its final tube-climbing score.

Some mice attempted to climb only at night, others as soon as they were placed in a cylinder, and still others had occasional daytime periods of wakefulness, in addition to their nocturnal activity periods, during which they would attempt to climb. The length of the test periods for the individual animals ranged from a single day to three weeks.

Although all of the mice learned to escape from the cylinder by climbing the tubes, a few at some advanced stage of the experiment developed a lack of inclination to do so. When this disinclination persisted, such individuals were eliminated without being scored. If a mouse which had succeeded in climbing a certain number of tubes attempted only weakly, or not at all, to climb the next in the series, it was rechecked to determine whether it was actually unable to climb the tube or had merely lost its incentive to escape. Rechecking was accomplished by reintroducing a means of escape well within the animal's demonstrated ability to climb. There is no evidence that elimination of the mice which had lost their incentive to climb affected in any way the experimental results. All of them had climbed at least one tube, and some several, before they were eliminated, and their climbing activity gave no indication that they differed in ability from other representatives of their respective forms.

A tendency to jump, rather than to climb, out of the cylinder, was exhibited by several of the mice. This was suppressed in large measure by the use of the tallest cylinders. A few mice, however, having once developed the habit of successful escape by jumping to the landing platform, could not be retrained in a reasonable length of time to escape by climbing even when one of the tallest jars was used. They would persist for a time in trying to jump to the top of the jar, but finally, after repeated failures, would settle down and make no further effort. Whenever a mouse could not be retrained to escape by climbing, it was eliminated from the experiment.

Since this experiment was conducted over a long period of time and in three different rooms, there were several variable factors. In view of the more or less comparable amount of variability, however, in each of the three rooms and because the mice were free to perform whenever conditions suited them, it seems likely that any environmental differences which existed were of negligible importance. Any slight effect the variables may have had was offset, furthermore, by the purely haphazard placement of a mouse in any particular room and by the proportional representation in any given location.

The mean climbing scores of the individuals tested in each form are listed, together with the means for body measurements and age in Table V. Since there were no significant differences in performance between males and females, the sexes have not been treated separately. Inspection of Column 3 of the table reveals the wide differences that existed among the forms in the mean number of tubes climbed. It is of particular interest that, in mean achievement, the four terrestrial forms, leucocephalus, blandus, bairdi, and nebrascensis, made the four lowest scores; the five semiarboreal forms, gracilis, truei, noveboracensis, nasutus, and oreas, the highest; and rubidus, from an intermediate type of habitat, an intermediate rank. Thus, the semiarboreal forms are demonstrably better able to climb tubes of greater diameter at the stated degree of roughness than are the terrestrial forms. The terrestrial forms climbed only the tubes of smallest diameters; rubidus climbed those of smallest diameters plus some of larger diameter; while the semiarboreal forms climbed not only the small tubes but nearly all of the larger ones as well.

In order to determine the significance of the different climbing abilities of the several forms of peromyscus tested, the mean climbing score of each form has been compared with that of every other form. The probability ratings of these comparisons, as determined by the use of t values, are given in Table VI. On the basis of the probability ratings, the peromyscus tested tend to arrange themselves into at least four general, somewhat overlapping, classes with regard to ability to climb the tubes of progressively greater diameter: (1) The terrestrial leucocephalus, which differs significantly from all other forms except blandus (also terrestrial). (2) The three terrestrial forms, blandus, bairdi, and nebrascensis. Two of them differ significantly from leucocephalus and all differ significantly from all the semiarboreal forms but not from rubidus. (3) Rubidus, which differs significantly both from the semiarboreal forms and from leucocephalus. This significance reaches the 1 per cent level of probability, however, only in comparison with two means, one at each end of the range of means. In general, rubidus, in this particular experiment, tends to align itself more closely with the terrestrial than with the semiarboreal forms. (4) The semiarboreal forms, gracilis, oreas, noveboracensis, truei, and nasutus, all of which differ significantly from all of the terrestrial forms tested, as well as from rubidus. There can be no doubt, therefore, that the differences in tested climbing ability between the semiarboreal and the terrestrial forms are of considerable magnitude.

Correlation of tube-climbing ability of the total number of mice tested (83) with body length, tail length, foot length, weight, and age gives r values of .70, .81, .77, .59, and -.01, respectively. All of these correlations, except that of ability with age, are highly significant. The

TABLE V

Means and Standard Errors for Tube-climbing Ability, Body Measurements, and Age of Peromyscus that Climbed Tubes of Uniform Roughness but Varying Diameter

Body dimensions recorded in millimeters; weight, in grams; and age, in weeks.

Species and Subspecies	Number of Mice Tested	Number of Tubes Climbed	Body Length	Tail Length	Tail Length/ Body Length	Foot Length	Foot Length/ Body Length	Weight	Age
polionotus leucocephalus . . .	10	3.1±0.28	79.80±1.36	55.10±0.92	0.69	18.34±0.23	0.23	13.6±0.55	61.2±10.32
maniculatus blandus	7	4.3±0.61	93.00±2.04	66.29±2.00	0.71	19.97±0.27	0.21	21.1±1.13	64.7±12.28
maniculatus bairdi.	11	5.2±0.38	87.82±1.07	72.45±0.76	0.82	18.53±0.14	0.21	19.1±0.98	82.5±11.80
maniculatus nebrascensis . . .	8	5.3±0.31	88.13±1.25	66.88±1.86	0.76	19.29±0.18	0.22	19.4±0.79	67.1±8.40
maniculatus rubidus	8	6.0±0.57	88.50±2.69	90.88±1.57	1.03	20.46±0.25	0.23	18.6±0.81	84.8±21.12
maniculatus gracilis	9	7.6±0.24	95.33±1.68	99.33±1.89	1.04	21.46±0.20	0.23	22.4±0.98	69.2±8.64
truei truei.	7	7.7±0.15	96.86±1.26	91.29±3.80†	0.94†	22.17±0.20	0.23	25.7±0.76	41.4±13.78
leucopus noveboracensis. .	7	7.9±0.14	98.00±2.52	97.86±2.23†	1.00†	21.33±0.34	0.22	22.6±1.10	69.1±19.65
maniculatus oreas	6	8.0±0.00	93.33±1.12	110.17±2.89	1.18	23.18±0.18	0.25	22.3±1.07	53.7±12.86
nasutus nasutus	10	8.0±0.00	99.80±1.11	107.50±4.73†	1.08†	22.79±0.14	0.23	29.2±1.42	85.4±17.09

† Measurement includes one or more mice with incomplete tails.

TABLE VI

Probability Ratings for Comparisons of Mean Tube-climbing Scores (Table V) of Peromyscus

The probability that any two means represent two populations of the same mean climbing ability is read in the block connecting the names of the two forms considered. 0 indicates a probability greater than .05 (not significant); * indicates a probability of .05 to .01 (significant); and ** indicates a probability of .01 or less (highly significant).

Species and Subspecies	p. leucocephalus	m. blandus	m. bairdi	m. nebrascensis	m. rubidus	m. gracilis	t. truei	l. noveboracensis	m. oreas	n. nasutus
polionotus leucocephalus....	...	0	**	**	**	**	**	**	**	**
maniculatus blandus........	0	...	0	0	0	**	**	**	**	**
maniculatus bairdi.........	**	0	...	0	0	**	**	**	**	**
maniculatus nebrascensis...	**	0	0	...	0	**	**	**	**	**
maniculatus rubidus........	**	0	0	0	...	*	*	*	*	**
maniculatus gracilis	**	**	**	**	*	...	0	0	0	0
truei truei	**	**	**	**	*	0	...	0	0	0
leucopus noveboracensis....	**	**	**	**	*	0	0	...	0	0
maniculatus oreas	**	**	**	**	*	0	0	0	...	0
nasutus nasutus	**	**	**	**	**	0	0	0	0	...

correlation of body length with climbing ability seems to be an important one, particularly with respect to span; for in general the longer the body, the longer the appendages. As long appendages can reach farther around the large tubes than can short appendages, the long-limbed mouse is better able to embrace the tube. Observations confirmed that a long-bodied, long-limbed nasutus is able to reach considerably farther around a tube of large diameter than is a relatively short-bodied, short-limbed leucocephalus, which cannot utilize as large an arc as nasutus and is unable, therefore, to brace its body as firmly against the tube. In effect, leucocephalus is required to climb a flatter surface than is nasutus.

Although the tail was pressed closely against the tube during difficult ascent, somewhat as a prop, there is no evidence that such use of the tail affected appreciably the tube-climbing scores of the mice. Twenty mice, two from each form, were tested with their tails and later retested without them. The 20 mice climbed 127 tubes before tail removal and a total of 115 tubes afterward. As a check, nine other mice, including an individual of each form except truei, were tested and retested in the same manner but with their tails intact in both tests. The nine mice climbed 57 tubes in the first test and 56 in the second. The difference in the numbers of tubes climbed by each group in the two tests is not statistically significant (chi-square equals 0.13). It seems unlikely, therefore, that the tube climbing was much affected by the tail lengths despite the very high correlation (r equals .81) between ability and length of tail.

Presumably, a long foot presents a greater grasping surface than a short foot; and a foot which is not only absolutely longer but relatively longer should be of still greater advantage in grasping. The highly significant correlation (.77) of climbing ability with absolute foot length has already been noted. The r value for correlation of climbing ability with the foot length-body length ratio in all individuals of the 10 forms is only .11, which, although positive, falls considerably short of significance. The corresponding r value for all individuals (49) of the six subspecies of maniculatus, however, is .32, which is of statistical significance.

That foot length and demonstrated climbing ability are here more closely correlated (r equals .77) than are body length and climbing ability (r equals .70) may be due to chance. It suggests, however, either that the demonstrated ability is dependent even more on absolute foot length than it is on absolute body length or that the size of both body length and foot length is controlled in large measure by general growth factors. Since few mice were tested and the measurements used do not lend themselves well to the determination of general or local growth factors, it can be stated here only that a highly significant correlation exists between demonstrated climbing ability and both absolute body length and absolute foot length.

The role of weight in climbing performance is difficult to ascertain. The weights of the mice used fall within the range considered normal for their forms as reared under laboratory conditions. When all individuals of the 10 forms are lumped in making the determination, the correlation value (.59) between weight and the number of tubes climbed is highly significant. Within a few of the forms there is evidence of a negative correlation. This attained significance only in bairdi, in which it amounted to —.69. Weight and body size have a general correlation in peromyscus (Table V), as in most animals, and mice of the forms with large body size usually demonstrated greater climbing ability than did those with small size. Consequently, it may be that the high correlation between weight and climbing ability (mice of all 10 forms lumped together) was due primarily to the dependence of weight on body size and that, if all other factors could be made equal, the less heavy of two mice would attain the higher performance score. For example, a particular leucocephalus, because of its relatively small size rather than its light weight, might be less able than a nasutus to climb a certain tube; but this same leucocephalus, chiefly because of its lighter weight, might be better able to climb the specified tube than another leucocephalus of the same body dimensions but greater weight.

Because of the general nature of this experiment the relative importance of body length, tail length, foot length, and weight in the climbing performance of an individual mouse cannot be determined. Each form is represented by only a small number of individuals; there is considerable individual variation in most of the measurements employed; and climbing ability depends on not one, but many, interdependent and diverse factors. The lumping together of the several forms is justified only in the determination of certain general correlations, for different species exhibit differences in body proportions other than those involving foot length and tail length (Clark, 1941). The lumping together of individuals of different subspecies of the same species is open to the same criticism, even though the number of significant subspecific differences in body proportions may be assumed to be less than the number of significant differences in body proportions that distinguish the species.

In conclusion, it may be stated that, whatever the relationship of body proportions to the type of climbing ability tested is, and it is highly complex, all of the semiarboreal forms proved better able to climb the tubes of greater diameter at the selected degree of roughness than did the terrestrial. Each semiarboreal form tested achieved a mean climbing score significantly higher than that of any terrestrial form. Rubidus, the intermediate in habitat, was intermediate also in climbing ability.

3. Climbing Tubes of Uniform Diameter but Progressively Lesser Roughness. -- The third experiment of this group, which is very similar to the second, was designed to measure the comparative ability of the mice to climb vertically on tubes which differed from one another only in degree of roughness. Evidence that roughness of surface affects the performance of mice was given in the trunk-climbing experiment above as well as in preliminary tests which involved the use of roughened tubes. The conditions and apparatus were the same as those in the second of these experiments except for the use of a different series of tubes. The four tubes employed in scoring each measured 44.5 mm. in diameter, but represented a graded series of progressively decreasing roughness. This was achieved by covering the tubes with 150-, 220-, 320-, and 600-mesh Crystolon, respectively. The 600-mesh, which is the

most finely powdered Crystolon, is comparable in fineness to dusting powder. The mice tested, for the most part, were the same as those of the preceding experiment. A few animals, for reasons due entirely to chance, were used in only one of the two experiments.

The results of this experiment, presented in Table VII, are remarkably similar to those of the preceding one (see Table V). Although the progressive order of mean achievement differs somewhat in the two experiments, the four terrestrial forms, as before, made the four lowest scores, the five semiarboreal made the highest scores, with rubidus maintaining its intermediate position. The probability ratings obtained by comparing the several performance means are given in Table VIII. As in the prior experiment the ratings fall into four groups: (1) Leucocephalus, in which the mean climbing score differs significantly from the mean scores of all other forms except nebrascensis and blandus. (2) Nebrascensis, blandus, and bairdi, all of which differ significantly from all of the semiarboreal forms in mean performance and one of which (bairdi) differs also from leucocephalus. A difference significant at the 5 per cent level exists also between the means of nebrascensis and rubidus. (3) Rubidus, which differs significantly in mean performance from all other forms but blandus and bairdi. This significance, however, barely reaches the 1 per cent level when considered with reference to the semiarboreal forms oreas, noveboracensis, and truei, and is between the 5 and the 1 per cent levels with reference to the terrestrial nebrascensis. (4) Gracilis, oreas, noveboracensis, truei, and nasutus, the performance means of which differ very significantly from those of all of the other forms. Mice of the semiarboreal forms, then, may be said to have demonstrated markedly greater ability to climb the relatively smooth-surfaced tubes than do those of any of the other forms.

Just as in the preceding experiment, highly significant positive correlations exist between demonstrated ability and body length, tail length, foot length, and weight, respectively, when all individuals of the 10 forms are lumped together in determining the correlations. The general agreement of correlation trends in the two experiments is not unexpected inasmuch as the mean body measurements and the comparative abilities, as indicated by statistically significant differences in performance means, are very similar.

Some general conclusions to be drawn from the results of the two tube-climbing experiments are (a) that the ability in forms of peromyscus to climb vertically placed objects is limited by both progressively larger diameter and progressively greater smoothness of surface of those objects and (b) that vertical-climbing ability in the forms studied is definitely correlated with the general type of natural habitat and presumably also with the general type of natural habit. Mice of the semiarboreal forms, therefore, should be better able to climb a greater variety of objects in nature than terrestrial mice, and rubidus individuals should be neither so able as the semiarboreal mice nor so unable as the terrestrial ones.

TABLE VII

Means and Standard Errors for Tube-climbing Ability, Body Measurements, and Age of Peromyscus that Climbed Tubes of Uniform Diameter but Varying Roughness

Body dimensions in millimeters; weight in grams; and age in weeks.

Species and Subspecies	Number of Mice Tested	Number of Tubes Climbed	Body Length	Tail Length	Tail Length/ Body Length	Foot Length	Foot Length/ Body Length	Weight	Age
polionotus leucocephalus...	10	1.8±0.10	79.50±1.37	55.00±0.79	0.69	18.35±0.19	0.23	13.6±0.65	50.2±11.34
maniculatus nebrascensis ...	8	2.1±0.23	87.75±1.56	66.50±1.95	0.76	19.21±0.21	0.22	18.9±0.94	66.0±9.47
maniculatus blandus	7	2.1±0.34	90.86±2.67	68.71±1.66	0.76	20.16±0.30	0.22	20.8±1.43	52.6±11.23
maniculatus bairdi..........	12	2.4±0.19	88.00±1.35	71.50±0.88	0.81	18.29±0.12	0.21	19.4±0.97	92.1±12.15
maniculatus rubidus	9	3.0±0.29	90.89±2.28	92.33±1.70	1.02	20.67±0.90	0.23	20.2±1.18	94.3±18.16
maniculatus gracilis........	11	3.9±0.09	94.82±1.37	98.36±1.71	1.04	21.45±0.16	0.23	22.9±0.88	63.8±8.15
maniculatus oreas..........	7	4.0±0.00	93.57±1.04	111.86±3.05	1.20	23.33±0.16	0.25	23.4±1.46	52.0±11.50
truei truei...........	7	4.0±0.00	96.86±1.06	90.43±3.36[†]	0.93[†]	22.47±0.23	0.23	24.7±0.78	48.4±16.26
leucopus noveboracensis..	7	4.0±0.00	99.43±2.45	97.57±1.69[†]	0.98[†]	21.23±0.32	0.21	22.6±1.10	71.3±19.12
nasutus nasutus	10	4.0±0.00	99.80±1.11	107.50±4.73[†]	1.08[†]	22.79±0.14	0.23	29.2±1.42	86.0±17.09

[†] Measurement includes one or more mice with incomplete tails.

TABLE VIII

Probability Ratings for Comparisons of Mean Tube-climbing Scores (Table VII) of Peromyscus

The probability that any two means represent two populations of the same mean climbing ability is read in the block connecting the names of the two forms considered. 0 indicates a probability greater than .05 (not significant); * indicates a probability of .05 to .01 (significant); and ** indicates a probability of .01 or less (highly significant).

Species and Subspecies	p. leucocephalus	m. nebrascensis	m. blandus	m. bairdi	m. rubidus	m. gracilis	m. oreas	t. truei	l. noveboracensis	n. nasutus
polionotus leucocephalus....	...	0	0	*	**	**	**	**	**	**
maniculatus nebrascensis...	0	...	0	0	*	**	**	**	**	**
maniculatus blandus........	0	0	...	0	0	**	**	**	**	**
maniculatus bairdi.........	*	0	0	...	0	**	**	**	**	**
maniculatus rubidus........	**	*	0	0	...	**	**	**	**	**
maniculatus gracilis	**	**	**	**	**	...	0	0	0	0
maniculatus oreas	**	**	**	**	**	0	...	0	0	0
truei truei	**	**	**	**	**	0	0	...	0	0
leucopus noveboracensis....	**	**	**	**	**	0	0	0	...	0
nasutus nasutus............	**	**	**	**	**	0	0	0	0	...

IV. Crossing of Gaps

1. Reaching across Gaps. -- Observation of the methods by which the mice crossed open spaces at elevated levels showed that if the gap was small and the mice had had no previous experience in crossing it, they usually reached across from one support to another. As the gap became larger and spanning it became more difficult, the mice jumped it when forced to make the crossing. Because of the tendency of the mice to jump gaps which were difficult but not necessarily impossible for them to reach across, the data on maximum reach are relatively few.

Horizontal Reach. Measurements of maximum horizontal reach were obtained by training the mice to cross successively larger gaps between two parallel rods. Each rod was of unpolished wood and one-fourth of an inch in diameter. Just prior to spanning the gap between the two rods a mouse would stand with all four feet on one rod and stretch its head forward toward the other, moving its vibrissae noticeably. In crossing, a mouse usually placed its feet individually as in walking. The tail was not used as a prehensile organ but to help the animal balance on one rod while stretching forward toward the other.

The maximum horizontal reach of the 11 mice tested, representing seven of the forms, ranged from 6.5 to 8.5 cm. as measured at 5-mm. intervals. It averaged 7.0 cm. for the four terrestrial individuals and 7.6 cm. for the seven semiarboreal. In no instance was the reach greater than the body length of the mouse, averaging 83 per cent of the body length in the 11 mice tested. In the terrestrial mice it averaged 79 per cent of the body length; in the semiarboreal, 86 per cent. Both absolute and relative horizontal reach, then, are greater in the semiarboreal than in the terrestrial for the individuals tested.

Downward Reach. Measurement of maximum downward reach was obtained by using two glass tubes of 7 mm. in diameter roughened externally with 220-mesh Crystolon. The tubes were set so that the tip of the upper was directly above the tip of the lower and so placed that the mouse had to proceed well toward the tip of the first tube in order to reach down to the second. The lower tube was terminated by a wooden cylinder, roughened by applying two rings of adhesive tape. This cylinder, approximately 35 mm. in length and 15 mm. in diameter, served as the landing platform toward which the mouse reached from above. The gap between the axes of the tubes was progressively increased by 15 mm. intervals. When a mouse reached down with its forefeet, it continued to hold on to the upper tube with its hind feet and, on the greater reaches, it flexed its tail about the upper tube. The apparatus and the downward reaching of the mouse are illustrated in Plate VII, A-T.

The maximum downward reach of the 11 fully tailed mice tested, representing all the 10 forms, ranged from 7.0 to 11.5 cm., as measured at 15 mm. intervals. It averaged 8.1 cm. for the four terrestrial individuals and 10.7 cm. for the six semiarboreal mice, and was 8.5 cm. for the single rubidus. The performance of an additional mouse, a gracilis with amputated tail, gave a value of only 7.0 cm. The maximum reach of the tailless gracilis was 1.1 cm. below the average for the four terrestrial mice, 3.7 cm. below the average for the six semiarboreal, and 4.5 cm. below the maximum reach of its tailed littermate of the same sex. Although these results are based on a very small number of mice, they do suggest that tail length is of considerable importance in assisting the mice to descend from one tube to another.

The maximum downward reach of the 11 tailed mice averaged 1.06 times their respective body lengths. The ratio of maximum reach to body length averaged 1.13 in the six semiarboreal individuals and 0.98 in the four terrestrial, and was 0.96 for the single rubidus and 0.80 for the single tailless gracilis. The tailless mouse had the lowest of any of the individual ratios. The maximum downward reach is shown, therefore, to be greater, in both absolute and relative terms, than is the maximum horizontal reach of the mice. When the animals hang downward from the upper support, while reaching toward the lower, they are obviously able to span greater gaps than when reaching forward across the space between horizontal rods.

In reaching toward the lower support with their forefeet the mice hung on to the upper one with their hind feet, assisted by their flexed tails. As soon as the forefeet had made secure contact below, an animal released its foothold above. It then made use of its tail to retard the rate of falling of the hind quarters by maintaining a gradually diminishing hold on the upper support (Pl. VII, G-K). The performance of the mice shown in Plates V, C-F, L-R, and VII, E-K, in comparison with that of the mouse shown in Plate III, F-K, gives some idea of the greater effectiveness of a relatively long tail, as distinguished from a shorter one, as an aid to successful descent in peromyscus. The longer tail not only renders the dropping of the hind quarters of the mouse more gradual, but facilitates more accurate placement of the hind feet on the lower support.

In reaching downward across small gaps the mice placed their four feet one after the other on the lower support, the two forefeet being usually followed by the two hind feet (Pl. VII, N-T). In the spanning of large gaps, however, both hind feet were released almost simultaneously from the upper support once the forefeet had taken hold of the lower one (Pl. VII, I-K).

Upward Reach. No measurements were made of maximum upward reach, but it was observed that some of the mice, when reaching directly or almost directly upward, could span gaps which slightly exceeded body length. The mice stood on their hind feet and thus gained height. The tail usually functioned here like the third leg of a tripod, to maintain balance, as the animal stood on its hind feet and stretched upward with its forefeet.

In crossing from one to another of two supports the mice behaved very cautiously, particularly so if the gap to be spanned was approximately more than half the body length of the mouse concerned. Crossing of larger gaps was always preceded by investigatory movements of the vibrissae, and often the mouse repeatedly extended a forefoot toward the second support before it finally made the crossing. Most of the mice returned to the first support several times before they demonstrated their maximum reaching ability, and it was usually only under compulsion that the larger reaches were made.

2. Jumping across Gaps. -- Although the mice could be trained to jump considerable distances from one support to another, they did surprisingly little spontaneous jumping under the experimental conditions. Their exploration of artificial and natural branches was usually cautious. In progressing along branches the mice often reached from one branch to another, but rarely jumped unless trained to do so. Nelson (1918: 524) reported that he had several times observed mice of the genus Peromyscus running up and down the branches of a small leafless tree and "leaping from twig to twig with all the active grace of tiny squirrels." He wrote that they "appeared to be racing about in pure playful enjoyment of the exercise." None of the peromyscus studied here exhibited any such squirrel-like behavior and it seems more likely that under natural conditions the mice jump from branch to branch only in emergencies.

The instances of spontaneous jumping observed in the laboratory occurred for the most part either when the mice were attempting to escape from some piece of apparatus or when they were greatly excited. Occasionally, mice jumped from elevated apparatus, often directly toward a nearby object. Most other jumping observed, however, was by the mice confined to the tall laboratory cylinders in the tube-climbing experiments. The most spectacular jumps were made by two mice (one truei and the other blandus), both of which jumped 30 inches upward to the rim of a glass cylinder only 8 1/2 inches in inside diameter.

In one instance a leucocephalus jumped accurately a 5-inch distance from the top of an aluminum igloo to the upper edge of a vertically placed piece of transparent plastic sheeting 1 mm. thick. The mouse made a perfect landing midway between two paper clips fastened to the sheeting. (It is possible that the clips, which were about 4 inches apart, served as visual guides.) The edge of the plastic sheeting was about 2 1/2 inches higher than the top of the igloo. In another instance a blandus jumped horizontally from a wooden block to the adhesive-tape-covered rim, approximately 6 mm. thick, of a laboratory cylinder. The animal jumped 5 1/2 inches and landed perfectly. Later, when the cylinder was moved a little farther away, the mouse made a similar jump of 6 inches. Jumps toward larger objects were more common, however, and several mice were seen to jump from an elevated object onto a nearby brick wall or onto a large-diametered tree trunk. These jumps, observed in both noveboracensis and gracilis, averaged about a foot in distance and were made either slightly upward or slightly downward.

Despite the instances described, spontaneous jumping was relatively infrequent. Nevertheless, mice of all the forms could be trained to jump. The training procedure entailed progressively increasing the distance between two supports, initially placed close together so that the mice could easily reach from one to the other. As the distance between the supports was made successively greater, at some point the mice resorted to jumping across the gap. Experiments using two unpolished wooden rods of 1/4-inch diameter showed that the mice could be readily trained to jump upward or downward as well as horizontally. No attempt was made to determine the maximum jump upward or downward at various angles, but measurements were made of the maximum horizontal jump for at least one individual of each form.

The apparatus employed in determining the maximum horizontal jumps of the mice consisted essentially of two parallel wooden rods, each 6 inches long and one-fourth of an inch in diameter. The rods were 28 inches above the floor, and each rod was attached to an elevated platform. On each of the platforms was placed an igloo baited with a sunflower seed.

The animals were tested in dim light, a single 10-watt bulb in an overhead ceiling fixture. At the beginning of each test the rods were placed close together, with axes parallel, at a distance of 2 cm. A mouse was placed under an igloo. After two minutes the igloo was slowly raised and very little time was usually required for the mouse, in exploring, to walk or run from one rod to the other. The igloo was then returned to the first platform, the sunflower seed replaced if eaten, and the rods moved 5 mm. farther apart. Since this procedure was performed repeatedly it soon became so familiar to the mouse that it usually went directly to the starting rod upon raising of the igloo and crossed over. As the distance between the rods became appreciably greater the mouse resorted to jumping from rod to rod. Once the mouse had learned to jump across the gap, it was possible, as long as the distance was easily jumped by the mouse, to increase the distance between rods by more than 5 mm. each time. The exact amount of increase between rods on successive crossings depended upon the performance of the individual. When a certain distance was jumped with difficulty, thereafter the distance was never increased by more than 5 mm. Whenever a mouse fell in attempting a jump, the rods were again placed close together and the mouse once more presented with a series of successively greater reaching and jumping distances. When the mouse had thrice worked up to distances so great that it fell to the ground, either in jumping short of the second rod or in slipping from the second rod in attempting to land, the test was discontinued for that day. This procedure was repeated on successive days until it was certain that the animal had demonstrated its maximum, or very close to its maximum, jumping ability. In the mice tested, it required from 5 to 15 days of this training before the maximum jump was attained. The range of actual test days was from 10 to 17.

Considerable variability in the behavior of the mice was noted. Some always remained under the igloo until it was raised and then immediately jumped across to the other rod. Others spent little time in the igloo and explored the platform freely between jumps. Much urging was necessary before most of the mice would jump the greater distances, although a few jumped them without being impelled by the raising of the igloo. While there was a certain amount of variability in the behavior of any one mouse from time to time, it was less than between any two individuals tested.

In jumping the mice seemed to depend not only upon vision but also upon an awareness of the degree of success achieved in the previous jump. When a mouse had barely succeeded in jumping a certain distance, it generally expended a little more effort in the next jump, whereas a mouse which had greatly overjumped expended less effort. That the mice sometimes seemed to judge distances more by kinaesthetic cues from the previous jump than by visual cues was indicated by the overjumping of certain mice when the rods had been moved closer together immediately following a successful jump. The exact nature of the interplay between visual, kinaesthetic, and other cues was not determined. It can only be stated here that both the visual and kinaesthetic seemed to be of importance in guiding the jumping of the mice from rod to rod. It is possible, too, that echolocation (Griffin, 1944) may have been employed by the mice.

During the jump the forefeet were extended forward. The hind legs, extended somewhat posteriorly immediately following the take-off, were gradually pulled forward under the body as the animal approached the second rod. The movements of the appendages were similar to those illustrated in Plate II, B-K. Usually, the tail was carried straight behind or slightly upward, but was sometimes moved markedly up at the very beginning of the jump. The tail appeared to be of great importance in helping the mouse balance itself on the landing rod. The mice jumped straight forward from one rod to the other, and there was no indication that the tail was used as a rudder to direct the course. All jumps were made from a standing or crouching position on the starting rod and were, therefore, of the type known as the standing broad jump.

Fourteen mice were tested. Ten of them were one-year-old females, one representative of each form. The others were four littermate gracilis, two males and two females, two months old.

The maximum jumps made by the 10 year-old females (Table IX) ranged from 39.0 to 66.5 cm. The greatest jumps were executed by three of the semiarboreal individuals and the shortest by the four terrestrial. Intermediate jumps were exhibited by the semiarboreal oreas and gracilis and by rubidus. The average maximum jump (57.0 cm.) of the five semiarboreal mice is considerably greater than that (42.0 cm.) of the four terrestrial mice. The ratios of maximum jump to body length (Table IX) show that the distances jumped by the mice ranged from 4.47 to 6.79 times the body lengths of the individual mice. In general, the distances attained by members of the semiarboreal forms were relatively greater than those attained by the terrestrial, although there was some overlapping in relative performance.

The maximum jumps made by the four two-month-old gracilis (Table X) ranged from 48.0 to 53.0 cm. The average jump (51.3 cm.) of these mice differed only slightly from the jump (49.5 cm.) of the gracilis in the group of one-year-olds. There was no marked difference in the performance of the two sexes in the two-month-old gracilis group; the two females exceeded by only 2.5 cm. the average jump made by the two males. The ratios of maximum jump to body length among the four young gracilis are more variable than their absolute jumping distances. Such consider-

TABLE IX

Maximum Jumping Performance of Ten Peromyscus

Standing broad jump. One-year-old females.

Species and Subspecies	Maximum Distance Jumped (cm)	Ratio of Maximum Jump to Body Length
maniculatus bairdi	39.0	4.76
maniculatus blandus.........	42.5	4.47
polionotus leucocephalus.....	42.5	5.25
maniculatus nebrascensis....	44.0	4.54
maniculatus oreas	48.0	5.05
maniculatus rubidus.........	48.5	5.22
maniculatus gracilis	49.5	5.38
leucopus noveboracensis.....	60.0	6.45
nasutus nasutus.............	61.0	6.29
truei truei	66.5	6.79

able variability in this ratio among littermates suggests that it is less valuable as a measurement of jumping ability than the more uniform absolute jumping distance. It is worthy of note here that the four younger gracilis individuals were as proficient in jumping as the one-year-old, because under natural conditions two-month-old mice are entirely dependent on their own abilities to escape from predators and jumping proficiency could be of great usefulness to them when pursued.

The results of the experiment on jumping may be summarized as follows. Mice of all of the forms could be trained to jump horizontally from one rod to another through distances at least four times as great as their respective body lengths. In general, the maximum performance

TABLE X

Maximum Jumping Performance
of Four Peromyscus maniculatus gracilis Littermates

Standing broad jump. Two-month-old males and females.

Sex	Maximum Distance Jumped (cm)	Ratio of Maximum Jump to Body Length
Male	48.0	5.58
Female	52.5	6.03
Male	53.0	5.89
Female	53.0	6.39

of mice of the semiarboreal forms tested exceeded that of the terrestrial, both in actual distance jumped and in ratio of jumping distance to body length. Four two-month-old gracilis showed only slight individual differences in jumping ability and none of them differed markedly in ability from a single one-year-old gracilis. Although spontaneous jumping from branch to branch under natural conditions may be infrequent, it is nevertheless significant that, when forced to jump, semiarboreal mice can jump farther than the terrestrial mice.

V. Climbing on Small Branches

In peromyscus proficiency in climbing along small branches varies with the nature of the branch. The characteristics of a branch which most influence proficiency are hardness of surface, inclination, flexibility, accessibility of nearby branches, roughness of surface, and diameter.

1. Hardness of Surface. -- Because of the difficulty in maintaining surfaces of a given hardness at a uniform degree of roughness throughout a test period, no measurements were made of the proficiency with which the mice traveled along branches of various degrees of hardness. Nevertheless, it was evident that very hard surfaces greatly restricted the use of the claws of the mice. Hard surfaces impeded progress less on smaller branches which could be grasped readily by the digits than on those of larger diameter. Hardness was also of less hindrance to the mice when the branches were very rough.

2. Inclination. -- Branches which sloped upward at a given angle were more easily traveled than were like branches which sloped downward at the same angle from the horizontal. The mice always ascended and descended the sloping branches head first. The tail was sometimes flexed about an acclivous branch (Pl. VI, N) and occasionally used as a brace to prevent the mouse from slipping backward, but flexing of the tail about declivous branches, to keep the mouse from sliding forward, was more frequent. A flexed tail is capable of exerting considerable pressure on a branch, thereby acting as a brake. This use of the tail as a brake is illustrated in Plate VI, O, where a mouse is descending a freely hanging sash cord. The pressure of the tail against the cord is sufficient to cause a slight bending of the cord. Whenever a mouse slipped to the underside of a branch, either during ascent or descent, the tail was flexed over that branch to help support the suspended body of the animal (Pls. III, D-E; IV, G).

3. Flexibility. -- Observations of the locomotion of the mice, whether along artificial branches of baling wire covered with adhesive tape, natural branches denuded of twigs, or tape-covered fly rods, showed that all of them experienced a progressively greater difficulty in staying upright which was in rough proportion to the flexibility of the branch. In general, the heavier the animal and the greater its speed, the more the branch swayed; the greater the induced sway, the greater the difficulty of the mouse in maintaining its balance; and the more difficult it was for

the mouse to remain upright, the more the tail was used to help maintain that position.

In measuring the comparative abilities of the mice to travel upright along flexible branches, three adhesive-tape-covered fly rods of progressively increasing flexibility were employed. Each slightly tapered rod was approximately 2 1/2 feet in length and 5 mm. in diameter. Each rod was firmly attached at its larger end to an elevated platform upon which was placed an igloo with a sunflower seed within it. The free end of each rod was adjacent to another elevated platform also provided with an igloo and sunflower seed. Once the mice had been trained to proceed from platform to platform by crossing laths and roughened glass tubes, they were offered the flexible fly rods as pathways from one platform to the other.

Twenty mice were tested, one of each sex from each form. Each mouse was scored during its initial progression along the length of each of the three flexible rods and the scores recorded in terms of errors rather than of achievement as follows:

0 errors. Mouse progressed from attached end of rod to support at free end of rod without losing its balance.

1 error. Mouse fumbled once but regained its foothold. A fumble involved loss of footing of only one foot (almost always a hind foot), the body of the mouse remaining all the while above, or chiefly above, the rod. Fumbling movements are illustrated in Plate IV, B-D.

2 errors. Mouse fumbled two or more times, each time recovering its foothold.

3 errors. Mouse regained its upright position after slipping into a position wherein its body fell below the rod (Pl. IV, F-L).

4 errors. Mouse slipped two or more times but regained its normal position each time.

5 errors. Mouse slipped and did not regain its upright position. Of the mice which made five errors, some fell to the ground, some dropped to the ground, and some completed the crossing by pulling themselves across the rod in an upside-down position.

In crossing a rod the mouse was given a score corresponding to its maximum error rating. Thus, a mouse which first fumbled but later slipped was given a score of 3 points; a mouse which recovered from 3 slips and then fell to the ground on the fourth slip was given a score of 5 points. Since 3 rods were included in each test, the maximum score which any mouse could make was 15 points. The minimum score of 0 indicated that there was no loss of balance on any of the 3 rods. That the mice experienced progressively greater difficulty in traveling along rods of increasing flexibility is evident from their total scores. The 20 mice made a total of 81 errors. Of this total, 9 errors were made on the least flexible, 30 on the more flexible, and 42 on the most flexible of the rods.

Average scores for the two individuals of each form tested are listed in Table XI, together with the average body weights and tail lengths of these same individuals. Since no marked sexual differences were revealed by the measurements, the sexes have not been considered separately. The scores show, as did extensive observations, that noveboracensis was best able to maintain its balance on the flexible rods (average score, 0.0) and blandus least able (average score, 12.5). Between these two extremes the individuals of the terrestrial forms nebrascensis, leucocephalus, and bairdi made fewer errors than some and more errors than others of the semiarboreal mice. The average score made by the semiarboreal mice, as a group, was 3.6 errors; while the average score of the terrestrial mice, as a group, was 5.6. This difference in performance between the two groups is not of statistical significance (t equals 1.06).

TABLE XI

Mean Errors in Locomotion by Peromyscus on Flexible Fly Rods and Mean Weights and Tail Lengths of Individuals Tested

Sexes not separated. Weight recorded to nearest gram; tail length, to nearest millimeter.

Species and Subspecies	Number of Mice Tested	Mean Number of Errors	Mean Weight	Mean Tail Length
Terrestrial:				
maniculatus bairdi	2	2.0	16	71
maniculatus blandus	2	12.5	20	67
maniculatus nebrascensis	2	5.0	17	64
polionotus leucocephalus ..	2	3.0	15	59
Intermediate:				
maniculatus rubidus	2	5.5	25	95
Semiarboreal:				
maniculatus gracilis......	2	3.5	19	96
maniculatus oreas........	2	1.5	21	116
leucopus noveboracensis ..	2	0.0	22	99
nasutus nasutus	2	8.5	29	107
truei truei...............	2	4.5	24	94

Except for blandus, mice of all of the terrestrial forms averaged lighter in weight than any of the semiarboreal. The difference in weight between the ten semiarboreal individuals, as a group, and the eight terrestrial individuals, as a group, is highly significant (t equals 3.44). The effect of heavier body weight on increasing the sway of branches and the difficulty of maintenance of balance has been mentioned. It is interesting, therefore, that the semiarboreal group, despite its significantly greater weight, made fewer errors in progression along the fly rods than did the terrestrial group.

The amount of swaying of a branch is affected not only by the weight of the mouse, but also by the speed of progression of the mouse along it. Rapidly moving mice propel their weights forward more forcefully than do slowly moving mice, thus producing a greater and more rapid bending of the branch. Since the mice which traveled most rapidly were usually the ones which made the fewest errors (only the semiarboreal noveboracensis and oreas traveled noticeably faster than the others), rate of progression alone is not an important factor in accounting for the relatively large number of errors made by the terrestrial mice.

In hind-foot length, the mean for the semiarboreal individuals was significantly greater than the mean for the terrestrial (t equals 5.95), but the ratio of hind-foot length to body length averaged the same (0.23) in both groups of mice. Moreover, the ratio which seems to be of even greater importance in the present experiment, that of foot length to body weight, actually was greater in the terrestrial group (1.14) than in the semiarboreal (0.98). It is doubtful, therefore, whether the absolutely greater foot length of the semiarboreal individuals gave them any advantage over the terrestrial individuals in this experiment.

A factor, in addition to body weight, which appeared to be of major importance in affecting maintenance of balance during progression along the flexible rods was tail length. The greater efficiency of the longer tail in the maintenance of balance was observed throughout. Not only could the tip of the longer tail circumscribe a greater arc, without involving the base of the tail to the extent of seriously dislodging the hind quarters, but a shift in balance which required circumscription of a large arc by a short tail required a much slighter movement by a long tail. The semiarboreal mice have markedly longer tails (Table XI) than the terrestrial mice and this difference in tail length between the two groups is highly significant (t equals 9.25). The longer tail of the semiarboreal forms seems, then, of primary importance in enabling these generally heavier animals to progress more proficiently than the lighter, shorter-tailed terrestrial ones. The difference in tail length between the two groups was sufficient, apparently, to more than compensate in performance for the greater swaying occasioned by the heavier semiarboreal mice.

Tail length in the semiarboreal group was not only absolutely longer than in the terrestrial group, but relatively longer in proportion to body length and to body weight. The ratio of tail length to body length averaged 1.07 in the semiarboreal individuals and 0.76 in the terrestrial individuals; that of tail length to body weight averaged 4.50 in the semiarboreal and 3.83 in the terrestrial. Although observations of the progression along flexible branches of mice differing appreciably only in ratio of tail length to either body length or body weight were few, the advantage in demonstrated ability seemed almost always to be possessed by the mice with the relatively longer tails. It seems probable, therefore, that in the progression of mice along flexible branches the longer tail is of greater value than the shorter not only because of its absolutely greater length, but also because of its greater length in proportion to both body length and body weight.

Several conclusions may be derived from these observations and measurements concerning the proficiency of the mice in traveling along flexible branches. Proficient locomotion of peromyscus on branches becomes progressively more difficult as the flexibility of the branch increases. Increasingly greater sway of a branch renders more difficult the maintenance of balance by the mouse. In progressing along a small flexible branch a heavy mouse produces a greater swaying than does a lighter mouse. The tail is used as a balancing organ in maintaining upright progression along a branch. In general, the long tails of the semiarboreal mice proved more effective as balancing organs than did the shorter tails of the terrestrial mice.

4. Accessibility of Nearby Branches. -- The progression of a mouse was frequently aided, when other branches were within reach, by pressing the tail against, or flexing it over, an accessible branch (Pl. VII, U-X). The mouse became aware of the exact position of such branches and their degree of flexibility by exploratory tail movements. The more twigs or branches that were accessible and the less flexible they were, the greater the use the mouse could make of them. The mouse availed itself of branches within reach usually only when progression became somewhat difficult. At these times greater movements of the tail increased the likelihood that it would come into contact with accessible branches.

In one experiment in which mice were required to descend a steeply inclined flexible branch bearing laterally projecting twigs, members of all 10 forms relied heavily upon flexing their tails over the twigs during descent. The tails were sometimes looped over the twigs at some distance from the branch, but were more commonly flexed over the twigs at their regions of insertion on the branch. Instances of looping the tail over a twig and then under an adjacent branch were also frequent.

In another experiment the mice were forced to cross horizontal tubes of progressively lesser degrees of both roughness and diameter. Paralleling each tube, above and to the side, was a taut wire. All of the mice used the wire when it was sufficiently close to them to be reached by their tails and when progression was sufficiently difficult to make the wire useful. Often, flexing the tail over the wire prevented a mouse from losing its balance. Lateral deviation of the hind quarters of the body came to an abrupt halt as the tail quickly tightened on the wire. Often a mouse held its tail so close to the wire during difficult progression that flexing over the wire or bracing against it was almost immediate when loss of balance seemed imminent. Not only was the wire used during unsteady progression, but it was used also to assist the animal in righting itself once it had slipped under the tube; the animal either pushed against or pulled on the wire with its tail in regaining an upright position. Although mice of all of the forms made use of the wire, when it was within reach of their tails, placement of the wire as far as 2 1/2 inches from the tube gave the longer-tailed semiarboreal individuals a tremendous advantage over the shorter-tailed terrestrial ones.

5. Roughness of Surface and Diameter. -- Decreased roughness of surface and decreased diameter of branch were both associated with greater difficulty of progression. The two factors are considered together,

not because they are more closely related than are any of the other variable characteristics of branches, but for convenience in describing the following experiment.

This experiment was designed to measure the comparative abilities of peromyscus of the several forms to maintain their balance on branches of relatively small diameter and relative smoothness. Artificial branches consisting of glass tubes which differed only in roughness, diameter, or both, were used. The sizes and roughnesses of the tubes chosen, on the basis of preliminary experiment, were those best suited to demonstrate the diverse abilities of individual mice to travel along hard-surfaced, nonflexible, twigless, horizontal branches. The tubes selected were not only sufficiently easy to cross that the majority of the mice could be trained to cross them upright, but sufficiently difficult that differences in crossing ability were apparent.

The apparatus consisted of two elevated platforms connected by the stick or tube to be crossed (Pl. I, C). Each platform, 14 inches in diameter and 27 inches in height, was supported from below by a metal rod. At the center of each platform was an igloo and within it a sunflower seed. The effective length of each tube was 22 inches and any tube was readily replaceable by any other. Six tubes, two each of three progressively lesser diameters and two degrees of roughness, were employed. The combinations and order in which they were presented are tabulated below.

Outside Diameter (mm.)	Crystolon Covering (mesh)
7	220
7	600
5	220
5	600
3	220
3	600

The tube-crossing tests were conducted under dim light in one of the compartments of the large experimental room. In the ceiling fixture of this compartment was a single 10-watt bulb and in that of the adjacent compartment a 15-watt. Each mouse was so placed on the platform that it could travel directly into the igloo. After a two-minute orientation period the igloo was slowly raised and the animal exposed on the platform. Usually the mouse soon crossed the 1-inch-broad stick leading from the first to the second platform and went into the second igloo. The first igloo was then lowered, a one-half-inch-broad stick substituted for the 1-inch stick, and the second igloo raised. Generally, the mouse went almost immediately to the stick and traveled back to the first platform. The igloo was lowered on the second platform, the first tube in the series substituted for the second stick, and the first igloo was again raised. This procedure was repeated until each of the six tubes had been crossed twice in succession by the mouse. Always the observer stood behind the igloo while raising it, with the doorway of the igloo facing the tube to be crossed. The sunflower seed was replaced whenever it had been eaten.

The method of scoring the tube crossings was the same as that used in scoring the flexible-fly-rod crossings (see 3, above); the scores, as there, were recorded in terms of total errors. The stick crossings, used to familiarize the animals with the apparatus, were not scored. Since each of the six tubes was crossed twice, there was a total of 12 scored crossings per mouse. The daily score of any mouse, therefore, could range from 0 points, for no loss of balance on any of the crossings, to 60 points, for irretrievable loss of balance on each of the crossings. The actual range of the daily scores was 0 to 45.

Preliminary experiments revealed considerably more day-to-day variability in performance than could be attributed to improvement due to training. Inasmuch as preliminary experiments had shown that the mice of the several forms responded similarly to training, it was believed that a mean score based on several daily tests might give a more valid measurement of the proficiency of a mouse than one based on a single test. The mean score of five successive daily tests, therefore, was decided upon as a measure of proficiency for each mouse. This particular number of tests was chosen because: (a) at the end of five tests none of the forms of mice had reached maximum tube-crossing proficiency and, since actual maximum proficiency for some forms was beyond the limit to be tested, the most proficient mice were thus placed at less disadvantage from a comparative standpoint than if more tests were used in calculating the mean; and (b) the use of five successive tests gave a mean which diminished the effect of day-to-day variability in performance and which was not, at the same time, influenced appreciably by effects on motivation as sometimes resulted from excessive training.

Eighty-one mice were tested. They included at least four individuals of each of the forms except rubidus. Of rubidus there was only one representative. Males and females were approximately equal in number. The age range was 13 to 109 weeks. Since neither sex nor age was associated significantly with differences in performance, results are presented as a single figure for each kind of mouse.

Just as the tube-crossing proficiency of any individual was represented by the mean of the number of errors made in five successive daily tests, so that of any form was represented by the mean of the mean daily scores of the several individuals of that form tested. The performance means for the forms, with the standard errors, are listed in Table XII. The data there show that each of the terrestrial forms averaged a greater number of errors than did any of the semiarboreal. In addition, the means of all of the semiarboreal forms, except nasutus, differ significantly from the means of all of the terrestrial forms. The mean of nasutus differs significantly only from those of nebrascensis (difference equals 7.6 errors; t equals 2.13) and noveboracensis (difference equals 5.5 errors; t equals 2.70). The score of the single rubidus was within the range of the semiarboreal rather than the terrestrial means.

The effect of training on improvement in performance was marked.

Of the total of 4939 errors made by the 81 mice in the course of the experiment, 1605 errors (32.5 per cent) were made the first day; 1023 (20.7 per cent) the second day; 864 (17.5 per cent) the third day; 778 (15.8 per cent) the fourth day; and 669 (13.5 per cent) the fifth day. Improvement was most pronounced immediately following the first test; the rate became more gradual thereafter.

TABLE XII

Tube-crossing Proficiency of the Several Forms of Peromyscus as Measured by Mean Errors Made in Crossing Selected Tubes during Five Successive Tests

Performance means and standard errors of individual means.

Species and Subspecies	Number of Mice Tested	Mean Errors in Performance
Terrestrial:		
maniculatus bairdi	8	15.2 ± 2.39
maniculatus blandus	6	19.5 ± 3.74
maniculatus nebrascensis	12	18.8 ± 1.93
polionotus leucocephalus	14	15.0 ± 1.35
Intermediate:		
maniculatus rubidus	1	9.0
Semiarboreal:		
maniculatus gracilis	21	6.9 ± 0.66
maniculatus oreas	6	9.1 ± 1.10
leucopus noveboracensis	4	5.7 ± 0.73
nasutus nasutus	4	11.2 ± 1.87
truei truei	5	7.3 ± 1.40

The total errors for each form are presented in Table XIII. In this table the totals for the second day have been combined with those for the third day and the totals for the fourth day with those of the fifth day. The distribution of errors shows that the various subspecies conform fairly well to the pattern of improvement cited above for the 81 mice as a group. The percentage of total errors made on the first day was, in general, considerably higher than that made on the second and third days and still higher than that made on the fourth and fifth days.

The arrangement of the data in Table XIII, in order of increasing percentage of total errors made during the first test, suggests, nevertheless, a difference in the rapidity of learning of the mice. The semiarboreal mice, on the whole, appear to have made more rapid improvement in tube-crossing proficiency than the terrestrial mice. The testing technique, however, was better adapted to more accurate measurement of the abilities of the terrestrial than of the semiarboreal forms. Since the most proficient mice could have crossed tubes of greater difficulty than those included in the experiment, such mice sustained a slight handicap and they might well be expected to make a larger percentage of their

TABLE XIII

Effect of Training on Tube-crossing Performance of Peromyscus, as Shown by Errors Made in Crossing Selected Tubes during Five Successive Tests

Species and Subspecies	Number of Mice Tested	First Test		Second and Third Tests (results combined)		Fourth and Fifth Tests (results combined)	
		Total Errors	Percentage of Errors	Total Errors	Percentage of Errors Per Test	Total Errors	Percentage of Errors Per Test
maniculatus blandus........	6	169	28.9	237	20.3	178	15.2
maniculatus nebrascensis..	12	329	29.2	443	19.7	354	15.7
maniculatus oreas	6	83	30.3	121	22.1	70	12.8
maniculatus bairdi	8	186	30.6	206	16.9	216	17.8
nasutus nasutus...........	4	71	31.8	96	26.5	56	12.6
maniculatus rubidus.......	1	15	33.3	20	22.2	10	11.1
polionotus leucocephalus...	14	364	34.5	400	19.0	289	13.7
maniculatus gracilis.......	21	262	35.9	263	18.0	204	14.0
leucopus noveboracensis...	4	45	39.5	35	15.4	34	14.9
truei truei	5	81	44.3	66	18.0	34	9.3
Total...............	81	1605	32.5	1887	19.1	1447	14.6

errors on the first day and a relatively smaller number on the succeeding days than would the less proficient mice. Consequently, that the scores of the semiarboreal forms improved more rapidly than did those of the terrestrial forms indicates, chiefly, greater arboreal ability rather than more rapid learning.

Factors other than the nature of the test undoubtedly affected the relative number of errors made by various individuals on successive test days. Among these may be noted certain differences in general behavior. For example, of all the mice tested several truei and leucocephalus showed the most marked difference in degree of excitement manifested during the first test and that exhibited during the last. A few which were greatly excited on the first test appeared very much at ease even on the second. This decrease in excitement may well account for their larger percentage of total errors made on the first day than might otherwise have been expected. The oreas mice, on the contrary, were noticeably calm even during the first test period. The first day they usually crossed the tubes directly, but on following days they tended to loiter along the tubes, often sitting there and washing their faces. In attempting to wash while sitting on a tube, they occasionally fumbled or slipped. Recovery was easy, and once an individual had slipped it behaved more cautiously thereafter. The relatively large number of errors made by oreas during the second and third tests is at least to some extent, therefore, a reflection of its general behavior. Furthermore, since oreas made many of its errors while loitering along the tubes, its performance mean somewhat underestimates its true tube-crossing ability.

From the foregoing discussion it seems evident that the data of Table XIII include no marked differences in learning ability among the several forms of mice tested. Although this experiment has not been designed to discover it, it is nevertheless possible that considerable individual and racial variability exists in peromyscus with regard to learning ability.

In the course of the experiment disqualification of certain individuals which were injured or did not adapt themselves to the experimental procedure became necessary. Of these mice, there were two which repeatedly jumped from part way across a tube to the opposite platform, one which persisted in somersaulting backward from the platform, and another which sustained a foot injury after the third day's test. Three mice which repeatedly dropped to the ground and five which repeatedly jumped were also eliminated. Elimination of certain individuals might be judged to affect the results of the experiment. But comparison of the incomplete scores of all the discarded mice with comparable parts of scores of mice of the same forms which had not been eliminated, showed remarkably slight differences in performance up to the time of disqualification.

Throughout the experiment environmental factors were controlled as carefully as practicable, and the mice were tested, in general, by the pairing technique. It seems unlikely, therefore, that whatever slight variability in environmental stimuli may have existed should have affected the mice of any one form more than another.

That decreased roughness and decreased diameter of small branches both limited the progression proficiency of peromyscus was a matter of common observation. Measurement of the effect on proficiency of the difference in roughness used was computed from the total errors that the 81 mice made in crossing the tubes of each roughness. Of the total errors (4939), 2059 (41.7 per cent) were made on the three tubes of greater roughness (220-mesh Crystolon covering) and 2880 (58.3 per cent) on the three of lesser roughness (600-mesh Crystolon covering). The smoother tubes are, therefore, shown to be more difficult to cross than the rougher ones. The conclusion is even more convincing in view of the fact that the smoother tube, at any given diameter, was in each case the second one crossed and the mice had thus had the benefit of previous experience.

Measurement of the effect on proficiency of the different diameters used was calculated from the total errors made by the 81 mice in crossing the tubes of each diameter. Of the 4939 errors, 344 (7.0 per cent) were made on the two tubes of 7-mm. diameter; 1003 (20.3 per cent) on the two of 5-mm.; and 3592 (72.7 per cent) on the two of 3-mm. Although the tubes were presented in order of decreasing diameter so that the mice had greater experience before crossing the smaller, the mice made an increasing percentage of errors as the diameter decreased. There can be no doubt that proficient locomotion along small branches must also become progressively more difficult as their diameters decrease, for differences in proficiency were marked with respect to a 2-mm. difference in diameter in the tubes employed.

In this experiment the tubes were made progressively more difficult to travel by combining decrease of roughness with decrease of diameter. The effect of this graded series of tubes in limiting the tube-crossing proficiency is to be seen from the total errors made by the mice on each of these tubes. Of the 4939 errors made by the 81 mice, 49 (1.0 per cent) were made on the first tube (7 mm. diameter, 220-mesh covering); 295 (6.0 per cent), on the second tube (7 mm. diameter, 600-mesh covering); 373 (7.6 per cent), on the third tube (5 mm. diameter, 220-mesh covering); 630 (12.8 per cent), on the fourth tube (5 mm. diameter, 600-mesh covering); 1637 (33.1 per cent), on the fifth tube (3 mm. diameter, 220-mesh covering); and 1955 (39.6 per cent), on the sixth tube (3 mm. diameter, 600-mesh covering).

The results of this tube-crossing experiment may be summarized briefly. The locomotion of peromyscus along small-diametered roughened tubes became more difficult with progressive decrease in diameter, progressive decrease in roughness, or both. The semiarboreal forms noveboracensis, gracilis, truei, and oreas were significantly more proficient in tube crossing than were the terrestrial forms leucocephalus, bairdi, nebrascensis, and blandus. Nasutus was more or less intermediate in proficiency, although its performance mean is closer in value to those of the other semiarboreal forms than to those of the terrestrial. The single rubidus individual was also closer to the semiarboreal in performance than to the terrestrial forms. With training, all of the mice of the several forms became more proficient, and there was little difference in the rate of improvement which could not be attributed either to difference in arboreal ability or to difference in general behavior. Since proficiency in the progression of peromyscus along small branches is undoubtedly of great importance under natural conditions, it is most significant that the mice of the semiarboreal forms proved better adapted for such locomotion than those of the terrestrial forms.

VI. Effect of Tail Amputation on Climbing Proficiency

The use of the tail in climbing was described above under Climbing Behavior. Observations and previous experiments had shown that tail length is positively correlated with climbing proficiency in the mice. The object of this experiment, therefore, was to measure the effectiveness of the tail as an aid to proficient locomotion along small branches. In progression along such branches the tail functions chiefly as a balancing organ or as a prehensile organ which assists in the recovery of an upright position by the mouse if slipping occurs. The apparatus and procedure followed were the same as those of the immediately preceding experiment.

In the main part of the experiment the mice were divided into an amputation group and a control group. The amputation group consisted of 10 gracilis, 10 nebrascensis, and 10 leucocephalus. Their tube-crossing proficiency was tested on five successive days. The tail of each mouse was then amputated. After a one-month period of convalescence, by which time the wound had healed over completely, the 30 mice were retested in the same manner on five successive days. The control group consisted of six gracilis, four nebrascensis, and two leucocephalus, all with normal tails. Except for not amputating their tails, the controls were treated exactly like the mice of the amputation group and two series of tests run on them. The sexes were equally divided for each form in both groups. The ages of the animals ranged from 14 to 68 weeks. Since neither age nor sex was significantly correlated with differences in performance, no distinction has been made in presenting the results (Table XIV).

In the first series of tests the mean number of performance errors made by each of the three forms of the amputation group (prior to amputation) was similar to that of the corresponding form in the control group. Moreover, the difference between the mean of the amputation group and that of the control group of the same form was less than that between means of different forms. In the second series of tests the mean score made by the control mice of each form was considerably lower in each case than that made during the first series. That the mean scores of the controls were lower than those made during the first series is to be attributed not only to greater proficiency resulting from learning which was carried over, but to a continuation of the learning throughout the second series. After amputation, the gracilis mice made significantly more errors than they had made with tails intact (difference equals 7.8 errors; t equals 4.22); the nebrascensis showed practically no difference in mean performance after amputation; and the leucocephalus attained a mean

TABLE XIV

Effect of Tail Amputation on Tube-crossing Proficiency in Three Forms of Peromyscus

Performance means and standard errors of individual means.

Species and Subspecies	Number of Mice Tested	Mean Number of Errors in Performance		
		First Series of Tests	Second Series of Tests	
		Mice with Tails Intact	Mice with Tails Intact	Mice with Tails Amputated
maniculatus gracilis (amputation group)........	10	6.7 ± 1.07	....	14.5 ± 1.52
maniculatus gracilis (control group)...........	6	5.9 ± 0.60	2.6 ± 0.00	....
polionotus leucocephalus (amputation group)........	10	15.6 ± 1.63	....	13.1 ± 1.16
polionotus leucocephalus (control group)...........	4	13.7 ± 2.60	8.7 ± 1.32	....
maniculatus nebrascensis (amputation group)	10	18.2 ± 2.20	....	18.1 ± 1.70
maniculatus nebrascensis (control group)...........	2	20.3 ± 6.72	12.3 ± 5.52	....

score lower by 2.5 errors. This does not signify, of course, that nebrascensis and leucocephalus perform just as proficiently or more proficiently without tails as with them, but that the proficiency of nebrascensis and leucocephalus amputees was less affected by loss of the tail than was that of gracilis amputees. Although learning affected favorably the proficiency of all the mice, the amputees of the three forms averaged considerably more errors than did their racial relatives among the retested controls. It is quite evident, therefore, that removal of the tail did greatly handicap the mice in crossing the tubes.

As has just been noted, performance of the gracilis amputees was more affected by tail removal than was that of the other amputees. The gracilis controls made a significantly lower mean score on the second series of tests than on the first (difference equals 3.3 errors; t equals 4.76), whereas gracilis amputees made a significantly higher mean score than they had previously made with tails intact (difference equals 7.8 errors; t equals 4.22). Hence, taking the control group of gracilis as a standard, one would expect the gracilis amputees to make a mean performance score of approximately three points, if tail removal had no effect on their tube-crossing proficiency. But the actual mean score was 14.5 points, which indicates that the amputees presumably made four to five times more errors during the second tests than they would have had their tails not been removed. Similarly, it may be estimated that nebrascensis and leucocephalus made at least one and one-half and one and one-third times more errors, respectively, on the second series of tests than if they had still had their tails. These estimates offer further proof that, although tail removal reduced the tube-crossing proficiency of all three forms, gracilis suffered a far greater handicap than did either nebrascensis or leucocephalus.

The mean tail-length measurements, with the standard errors, for those individuals of the three forms which were included in the amputation group are listed in Table XV. Each tail-length mean differs very significantly from every other tail-length mean, the difference between the means of gracilis and nebrascensis being considerably greater (difference equals 31.40 mm.; t equals 15.91) than that between the means of nebrascensis and leucocephalus (difference equals 9.40 mm.; t equals 5.82). The mean length of the tail stub remaining after amputation varied only slightly and never significantly in the three forms. This virtually ineffective tail stub was in all instances so short as to be barely evident. Although amputees of the three forms were closely comparable in length of tail stub, they had originally been markedly different in length of tail.

A comparison of tail-length measurements with the estimated effects of tail removal on proficiency showed that the long tail of gracilis is a more effective aid in tube crossing than is the shorter tail of either of the other two forms. Furthermore, the tail of nebrascensis, which is somewhat longer than that of leucocephalus, is somewhat more effective than is the tail of that form. According to the performance means, the tube-crossing ability of leucocephalus was least affected by tail removal. The gracilis amputees attained a mean score more or less intermediate between the mean scores of the leucocephalus and the nebrascensis

TABLE XV

Means and Standard Errors for Body Measurements of Peromyscus of Amputation Group

Body dimensions recorded in millimeters; weight, in grams.

Species and Subspecies	Number of Mice Tested	Original Tail Length	Tail Length After Amputation	Body Length	Foot Length	Body Weight
maniculatus gracilis	10	96.10 ± 1.48	12.60 ± 0.92	95.70 ± 1.35	20.97 ± 0.29	21.7 ± 1.20
maniculatus nebrascensis......	10	64.70 ± 1.38	13.10 ± 0.72	88.20 ± 1.59	19.09 ± 0.16	18.5 ± 1.35
polionotus leucocephalus.......	10	55.30 ± 0.86	11.60 ± 0.45	78.40 ± 1.31	18.48 ± 0.15	14.5 ± 0.45

amputees, whereas before tail removal gracilis had a mean score significantly lower than that of either of them (difference equals 8.9 and 11.5 errors, respectively; t equals 4.54 and 4.71, respectively). On the other hand, the performance means of nebrascensis and leucocephalus differed more from one another after tail amputation (difference equals 5.0 error points) than before (difference equals 2.6 points). The longer tail of nebrascensis apparently compensated somewhat for certain other factors, as perhaps its greater weight, its relatively shorter hind foot, or both. The actual effects of other differences in body measurements on the tube-crossing proficiency of the mice cannot be assessed from the results, but the positive correlation of tail length with tube-crossing proficiency is marked.

As a part of this experiment the tube-crossing proficiency of several additional gracilis was determined. Four of these underwent whole-tail removal and four underwent half-tail removal. The mice were operated on approximately three months before they were tested, and at the time of testing ranged from 57 to 64 weeks in age. The sexes were equally divided in each group.

The performance means for the two additional groups of mice are given in Table XVI and, for comparison, the mean score attained by the 10 gracilis of the amputation group (prior to amputation) from Table XIV. In body measurements the mice of these three groups differed significantly only in tail length (see mean measurements, Table XVI). Comparison of performance means and tail-length means shows clearly the dependence of tube-crossing proficiency on tail length. The normal animals showed considerably greater proficiency than the half-tailed ones and the half-tailed more than the virtually tailless. The data given in the two tables show that the 10 tailless gracilis had a score (14.5 ± 1.52) during the second series of tests (Table XIV) more or less intermediate between that of the half-tailed mice (11.7 ± 1.78) and that of the no-tailed mice (21.0 ± 3.31), during their one and only series of tests (Table XVI). Therefore, given mice of comparable tail length, then those with the greater amount of training demonstrate the greater tube-crossing proficiency; whereas in mice with equal amount of training, proficiency is more or less dependent on a longer or shorter tail.

All of the previously described operations had been performed on animals which were at least six months old, so that at the time of the operation the animals had already learned to climb about in their cages with their tails intact. None of the mice, however, had received any previous training in climbing outside of their cages prior to the tube-crossing experiment. It seemed possible that mice which had never known the assistance of a tail might learn to climb as proficiently without their tails as did those animals which had always had them. The following experiment was carried out to ascertain whether mice which had never learned to use tails could perform as well as those which had become dependent upon the presence of a tail. Two litters of gracilis were employed. In the first litter of four mice, one male and one female were deprived of their tails at the age of 10 days, and one male and one female were left with tails intact. In the second litter, one

TABLE XVI

Effect of Tail Amputation on Tube-crossing Proficiency in Several Groups of Peromyscus maniculatus gracilis

Performance means and standard errors of individual means.

Class	Number of Mice Tested	Mean Tail Length (mm.)	Mean Number of Performance Errors		
			Mice with Tails Intact	Mice with Half Tails	Mice with No Tails
Mice of amputation group (Table XIV)................	10	96.10 ± 1.48	6.7 ± 1.07	....	....
Mice more than six months old at time of operation	4	54.00 ± 1.36	....	11.7 ± 1.78	....
Mice more than six months old at time of operation	4	15.50 ± 1.45	....	....	21.0 ± 3.31
Mice ten days old at time of operation..................	4	14.00 ± 1.42	....	....	14.0 ± 2.34
Unoperated littermate controls	3	93.67 ± 3.67	6.7 ± 1.39	....	....

male and one female underwent the same operation 10 days after birth, and the remaining one, a female, was kept as a control. (At the age of 10 days the mice are still unable to progress in an upright manner.) When these mice were three months old they were each given five successive daily tests in tube crossing. The performance means for these animals are listed in Table XVI. The mean of 6.7 ± 1.39 errors made by the three control mice of the two litters is closely comparable to that (6.7 ± 1.07) made by the 10 gracilis mice when tested with their tails entire. A mean score of 14.0 ± 2.34 errors was made by the four mice which had never experienced the assistance of the tail in locomotion. A difference between the means of the four tailless mice and the controls of 7.3 points indicates that the tube-crossing proficiency of the long-tailed gracilis was not due alone to learned dependence upon the tail, although this difference falls just short of significance (t equals 2.43; $N_1 + N_2$ equals 7). However, the difference between the mean score of 14.0 ± 2.34 made by the mice early deprived of their tails and that of 21.0 ± 3.31 made by the four which had already learned to use the tail as an aid to locomotion (difference equals 7.0 points; t equals 1.74) suggests, but does not prove, that some learned dependence upon the tail was involved.

Since learned dependence upon the tail appears to be involved, it is advisable to apply a correction factor to the previously stated estimates of tail-length effectiveness. A 50 per cent reduction of the difference between the scores made by gracilis individuals before and after amputation would certainly be more than adequate, on the basis of the scores made by the mice which had never learned to use their tails, to compensate for the learned dependence of a long-tailed mouse upon its tail. It is well within the realm of conservatism, therefore, to conclude that gracilis individuals, when deprived of their tails, make at least twice as many errors, exclusive of those presumed to be due to learned dependence upon the tail, in progression along the described tubes as might be expected if their tails were intact. Although there is no basis for determining the reduction factor needed to compensate for learned dependence on the tail in either nebrascensis or leucocephalus, certainly neither of these forms would be expected to exceed the previously stated estimates of tail efficiency. There can remain no doubt, therefore, that the long tail of gracilis is a more effective aid to progression along small tubes, simulating small branches, than is the shorter tail of either nebrascensis or leucocephalus.

In conclusion, differences in the performance of three forms of mice before and after tail amputation demonstrated that the tail was of great importance as an aid to proficient progression along artificial branches of small diameter and relative smoothness of surface. The long-tailed, semiarboreal form gracilis suffered a greater reduction in proficiency, after the tail was removed, than did either of the shorter-tailed, terrestrial forms nebrascensis and leucocephalus. Furthermore, individuals of gracilis which underwent whole-tail removal suffered a greater loss in proficiency than did those which underwent half-tail removal. It was estimated that, when deprived of their long tails, gracilis would make at least twice as many errors in tube crossing as would be expected if their tails were intact and also that, when deprived of their shorter tails, nebrascensis and leucocephalus would make no more than one and one-half times as many errors as would be expected if their tails were intact. Hence, although in all three forms the tail is of adaptive value in locomotion along small branches, the long tail of the semiarboreal gracilis is of greater adaptive value than is the shorter tail of either of the two terrestrial forms tested.

DISCUSSION

Within the genus Peromyscus certain forms are restricted fairly closely to semiarboreal habitats, while others are limited more or less strictly to terrestrial habitats. In general, the forms which live in the wooded areas have tails which are longer than those of the forms which occupy open types of habitat. The semiarboreal forms studied in this investigation were gracilis, oreas, noveboracensis, nasutus, and truei; the terrestrial, bairdi, blandus, nebrascensis, and leucocephalus. An additional form, rubidus, was represented by a stock derived from animals inhabiting an extensive area of brushland near Hood River, Oregon, a type of habitat which is somewhat intermediate between wooded and open country. Despite the general paucity of literature concerning the behavior of these forms under natural conditions, it was concluded that the terms "semiarboreal" and "terrestrial" could properly be applied to the habits as well as to the habitats of the forms so designated. It is not known whether the behavior of the Hood River rubidus in nature resembles more closely that of the semiarboreal or that of the terrestrial mice. Since the rubidus mice are more or less intermediate with respect to habitat, however, it was presumed that they are more or less intermediate in climbing behavior.

The measurements of the mice (Tables V and VII) show that in all of the terrestrial forms the tails were not only absolutely but also relatively, when compared with body length, shorter than in those of the forms known to be somewhat arboreal in habit. The tail length of the Hood River rubidus stock was closer to that of the semiarboreal than to that of the terrestrial forms. Absolute tail length of the rubidus was exceeded somewhat by that of all of the semiarboreal forms with the possible exception of truei (Table VII), and the relative tail length was surpassed by all of the semiarboreal forms except possibly truei and noveboracensis.

Structural modifications, if they are to be of maximum effectiveness in nature, must be accompanied by appropriate reactions and, as has been shown in this study, the arboreal adaptations of peromyscus involve modifications not only of body structure but of general behavior as well. In the absence of pathways to the ground the semiarboreal forms showed a greater tendency to remain for a given length of time on an elevated platform than did the terrestrial forms. Rubidus, which inhabits a transitional type of habitat, was more or less intermediate between the two groups in its response to elevation. Most of the semiarboreal individuals which failed to remain at the elevated level seemed to leave that position intentionally and gave evidence of awareness of their general position above ground. On the other hand, most of the terrestrial individuals which failed to remain aloft appeared to leave the elevated position accidentally and to show less awareness of the general relationship of the support to the ground. The semiarboreal mice seemed also to be more at ease on elevated apparatus and less anxious, when pathways to the ground were available, to progress immediately downward. The semiarboreal peromyscus, then, by virtue of their greater tendency to remain at elevated levels, their greater awareness of the elevation, and their greater ease in climbing about on elevated apparatus, exhibit behavior which is more appropriate to scansorial habits than is that of terrestrial forms.

The types of progression which may be employed by peromyscus under natural conditions fall into three general categories: vertical climbing, progression from one to another of two noncontiguous branches, and progression along branches. In each category the tail is useful to the progression of both the terrestrial and semiarboreal forms, but in each type of progression the semiarboreal forms are more proficient than the terrestrial. In mice of all the ten forms the tail was occasionally used as a prop during vertical ascent. In descent, it was often pressed closely against tree trunks, or tubes, and employed as a brake. During descent the degree of rotation of the hind limbs in all of the forms was somewhat less than that commonly observed in the arboreal squirrels.

Each of the five semiarboreal forms of peromyscus was able to climb a significantly greater proportion of a series of roughened vertical tubes of various sizes and roughnesses than was any of the four terrestrial forms (Tables V - VIII). Some natural, as well as simulated, vegetation proved particularly difficult for individuals of the terrestrial forms to climb. Certainly, the semiarboreal mice are able to climb effectively a great number of the available trees and shrubs of most habitats, a factor of primary importance in the use of these types of vegetation for food, nesting sites, and escape from predators. Therefore, there can be no doubt that the semiarboreal forms, since less restricted in their ability to use available vegetation, are less handicapped in climbing vertically under natural conditions than are the terrestrial forms.

In progressing from one to another of noncontiguous branches a peromyscus tends to be very cautious. When the two branches are close together the animals "whisker" the second branch carefully and then extend one foot forward to that branch. If the second branch yields very little under the extended foot, the crossing is usually completed. In no instance was the horizontal reach from branch to branch greater than the body length of the mouse concerned. But in reaching directly downward from one to another of two artificial inflexible branches, several mice were able to span gaps which slightly exceeded their respective body lengths, for the animals were able to hang by their hind feet and tails while reaching toward the lower branch. Here the tail appeared to be of considerable importance as an aid to supporting the weight of any mouse as it hung downward. By means of its gradually diminishing hold on the upper branch following release of the hind feet from that branch, the tail also retarded the rate of dropping of the hind quarters of the animal and thereby facilitated accurate placement of the hind feet on the lower branch. That the long-tailed forms were able to span greater downward distances, in comparison to body length, than were the short-tailed forms further indicates that the tail is an effective aid to this type of gap spanning. In maximum upward reach the mice, by standing on their hind feet as they reached upward, were able to negotiate distances which were slightly greater than their respective body lengths. Reaching was preceded by markedly cautious exploratory behavior in all instances in which a mouse progressed for the first time from one small branch to another and the gap between the branches was more than approximately one-half its body length.

Although mice of all of the forms could be trained to jump distances greater than four times their respective body lengths in traveling from one to another of two small supports placed at the same distance above ground, it is questionable whether spontaneous jumping from branch to branch plays an important role in the usual locomotion of peromyscus. Spontaneous jumping from support to support in the laboratory was observed in only a few instances despite ample opportunity. Moreover, since effective jumping in nature would presuppose the ability to locate precisely a second support, the question arises as to whether these chiefly nocturnal animals are able to see their targets clearly or whether they have to rely on special accessory sensory mechanisms comparable perhaps to those employed by bats. Possibly, jumping from branch to branch is resorted to in nature only in times of emergency. McCabe and Blanchard (1950), however, in their report of extensive field and laboratory observation of P. maniculatus gambeli, P. californicus californicus, and P. truei gilberti, stated that brilliant climbing and jumping distinguish gilberti from the other two forms. Hence, it is perhaps of significance that the most frequent and spectacular of the jumps that were recorded here were those of P. truei truei, which is closely allied to P. truei gilberti.

That certain mice of this genus may fall great distances without suffering any apparent injury was noted by both Cahalane (1939: 434) and Hamilton (1928: 65-66). Cahalane witnessed the falling of a specimen of Peromyscus boyli rowleyi from an oak limb 20 feet above ground. The mouse held its legs out stiffly while falling, landed upright, and immediately ran away. Hamilton noted several instances in which noveboracensis mice leaped, when pursued, from the fourth floor of a building to the pavement below. None of the recaptured mice showed any evidence of injury, and "one large female gave birth to four normal young two days after such a fall" (Hamilton, 1928: 66). Similar records of falling from considerable distances without apparent injury have been described for the common house rat and the red squirrel (Hamilton, 1928: 66), as well as for the fox squirrel (Allen, 1943: 220).

The rate of frequency of injury as a result of falling is a factor of considerable importance to animals of scansorial habits, although not all climbing mammals seem so well adapted to falling as do those described above. Of the three forms of peromyscus studied by McCabe and

Blanchard (1950: 94), maniculatus gambeli and truei gilberti can be dropped considerable distances without ill effect, whereas californicus californicus, an efficient climber, "is likely to bounce off intervening branches and often lands unrighted with a heavy and in one instance deadly impact." Carpenter's field study of the gibbon, an animal which is far heavier than any of the above-mentioned rodents, indicates that a high percentage of the captured gibbons showed healed bone fractures (Carpenter, 1940: 70). Carpenter believed these injuries to have resulted from falls, particularly from falls in which weak branches break beneath the weight of the animals.

In progressing horizontally along roughened tubes simulating small branches all of the semiarboreal forms of peromyscus demonstrated greater proficiency than the terrestrial, and a large part of this was owing to the greater length of the tail. Differences in performance of mice of three forms, before and after tail amputation, showed that the long-tailed, semiarboreal gracilis suffered a greater handicap, as a result of unlearned dependence on tail use, than that sustained by the terrestrial forms, nebrascensis and leucocephalus, which are shorter tailed. Gracilis amputees made at least twice as many errors in tube crossing as would be expected had their tails been intact, whereas nebrascensis and leucocephalus amputees made no more than one and one-half the expected number of errors. The longer tail of gracilis is, therefore, of greater value as an aid to progression along small tubes and branches than is the shorter tail of the terrestrial forms. Experimental results showed also that the long-tailed, semiarboreal forms, as a group, exhibited greater proficiency in traveling along flexible artificial branches of small diameters, even though their greater average body weight produced a greater swaying of the branches. The length of tail of the semiarboreal forms was sufficient to more than compensate for the greater swaying of the branches effected by the greater weight.

Although long tails were more effective aids to progression than short tails, mice of all of the forms studied showed marked use of the tail during locomotion along small branches. Use of the tail as a balancing organ was evident whenever balance became difficult, the tail movements serving to counterbalance the continuous shifts in the center of gravity of the body of the moving animal. Here again the greater effectiveness of the longer tail was evident; not only could the tip circumscribe a greater arc without seriously dislodging the hind quarters of the mouse, but a recovery of balance requiring only a slight movement of a long tail required a greater movement of a short tail. Thus, a long tail, as well as being able to do all that a short tail can, is capable of achieving a precision of balance unattainable by the short tail.

In addition to use as a balancing organ, the tail serves as a prehensile organ, a prop, or a tactile organ. The prehensility is apparent whenever a mouse attempts to recover its upright position after its hind feet have slipped from the upper surface of a branch. The tail is flexed over the branch and either helps brace the animal, while it pulls itself upright, or helps pull the mouse into the upright position. If another branch is within reach, the tail may be flexed over that instead, but used similarly. Employment as a prop is sometimes observed during times of precarious progression, when the tail is held tautly against a nearby branch in such a manner as to brace the unsteady body of the mouse against that branch, or during times of leisurely progression, when the tail, together with the hind legs, supports the animal as it raises the forelegs to wash, eat, or investigate. Tactile use is evident whenever the gently waving tail touches a nearby branch and then remains close to it, often even in contact, but not pressed against it. The tail is kept ready to press against or to flex over such a branch, should slipping of the hind feet seem imminent. As a tactile organ the tail informs the brain of the presence of nearby branches which may be used in time of need. As the mouse's progression becomes increasingly arduous, waving of the tail becomes more marked, and accessible branches are thus more likely to be located. Since the several functions of the tail are closely related, it is often difficult to isolate one from another, but instances of each of these four have been observed in which the long tail of the semiarboreal forms was more useful during locomotion along small branches than was the shorter tail of the terrestrial forms.

The foregoing discussion of tail use as related to the progression of peromyscus leads to further consideration of various relationships between body proportions and climbing ability. The tail-amputation experiments have demonstrated a positive correlation between tail length and proficiency in climbing along small artificial branches; and there are undoubtedly several additional relationships between body measurements and climbing proficiency. The rather widespread tendency, for example, of the semiarboreal forms to have hind feet which are both absolutely and relatively longer than those of terrestrial forms may be correlated in some way with climbing ability. Because of the impracticability of obtaining precise measurements of the feet of living mice and because, also, of the difficulty of isolating the foot-length factor in experiments designed to measure the comparative abilities of a relatively large number of forms of peromyscus, no persistent attempt was made to determine such a correlation in the present investigation. Moreover, in studying the relationship of foot size to climbing ability it would be necessary to consider the degree of development of the plantar tubercles, since these tubercles show considerable variation in prominence among the several forms studied. The consideration of foot size with regard to arboreal adaptation is complicated, too, by the fact that foot size may respond to the demands not only of arboreal activity, but of locomotion on loose sand. The latter type of adaptation has been suggested by Hayne (1950: 39, 51, 53) for leucocephalus and closely related coast-dwelling mice, all of which have longer hind feet than do closely related forms living inland on less sandy soil. Such an adaptation would be comparable in function to that so frequently noted in descriptions of Lepus americanus, the relatively large-footed snowshoe hare (Anthony, 1928: 483; Burt, 1946: 242; Cahalane, 1947: 583).

Body weight, as well as tail length, is related to climbing ability. A heavy mouse produces greater swaying of a small, flexible branch than does one of lesser weight. Greater swaying of the branch, in turn, renders the maintenance of balance more difficult. Weight may also affect other aspects of climbing. One obviously obese animal was unable to climb certain roughened vertical tubes, which several days later, after it had assumed a weight comparable to that of its cage-reared relatives, it climbed quite easily. Although mice which showed evidence of obesity were excluded from the experiments, the weight of any mouse nevertheless varied from time to time. Furthermore, since captive peromyscus are usually heavier than newly captured wild specimens, a fact first noted by Sumner (1932: 18), there is some question as to how accurately the weights of laboratory mice represent the weights of the same forms under natural conditions.

Relationship of body weight to climbing ability is extremely complex. In this study the semiarboreal forms were heavier, in general, than the terrestrial ones, greater weight being correlated with greater body size of the particular semiarboreal stocks used (Tables V and VII). Since the semiarboreal forms also exhibited greater climbing ability, in general, than the terrestrial forms, body weight showed a positive correlation with the climbing ability of the several forms. Within the form bairdi, however, was found a significant negative correlation (r equals -.69) between body weight and ability of the mice to climb roughened vertical tubes of progressively greater diameters. It may well be, therefore, that ability in this type of climbing is positively correlated with general body size and that weight, because it is generally dependent on body size, shows a similar positive correlation with the climbing ability in mice of marked differences in body size; whereas a negative correlation of this ability with weight is apparent only when abilities of mice of similar body lengths are compared.

It is evident from the experiments and observations described that the longer-tailed, semiarboreal forms surpassed the shorter-tailed, terrestrial forms in climbing proficiency, but the performance of the Hood River rubidus, of somewhat intermediate status, warrants separate discussion. The rubidus scores for jumping ability and crossing of roughened glass tubes fell within the range attained by the semiarboreal rather than the terrestrial forms (Tables IX and XII). Although each score for rubidus was based on the performance of only one mouse, extraexperimental observations of such performance by rubidus support their general validity. Since the Hood River rubidus aligns with the semiarboreal rather than with the terrestrial forms in relative tail length, these performance scores are in harmony with the general correlation between tail length and arboreal ability. In ability to climb roughened vertical glass tubes (Tables V and VII), however, rubidus was more or less intermediate between the terrestrial and the semiarboreal groups, and its scores were actually closer to those of the terrestrial than to those of the semiarboreal mice. One possible explanation for this apparent discrepancy is that body length, which showed a significant correlation with ability to climb roughened vertical tubes, is of primary importance in this type of performance. The average body length of the rubidus tested was more like that of the terrestrial than that of the semiarboreal forms (Tables V and VII). It may be that the small body size of rubidus, as of the gambeli studied by McCabe and Blanchard (1950), so facilitates its finding of ready refuge in incidental cover as to constitute in itself one of the chief adaptations for survival. McCabe and Blanchard, in discussing the importance of size and its relationship to mode of life, have pointed out that rodents but a little larger than gambeli must resort to such adaptations for survival as climbing or digging. Certainly, the results of this investigation favor such a conclusion to the extent that they show that it is, in general, the larger forms of the genus Peromyscus which demonstrate the better climbing ability. Other differences in body proportions, not yet studied, may offer information relevant to the climbing proficiency of rubidus. Clark (1941: Table 4) calculated that a stock of rubidus from Eugene, Oregon, had a relatively shorter femur, as compared with foot length, than did any of the other nine forms of peromyscus, including 41 different stocks and both terrestrial and semiarboreal forms. Since span appeared to be a very important factor in the climbing of the tubes, possibly rubidus, if the ratios of some or all of the long bones of its legs are smaller than the same ratios in the other forms studied, is somewhat handicapped by virtue of its relatively shorter legs. Whatever the explanation of the climbing ability of the Hood River rubidus is, this stock, although better adapted to arboreal habits than the terrestrial forms tested, is not so well adapted for scansorial performance as the semiarboreal forms studied. It is, moreover, evident that scansorial ability is facilitated by factors other than the mere possession of a long tail.

With regard to general habits, peromyscus may be regarded as terrestrio-arboreal, with some of its forms more arboreal than others. References to the arboreal activity of the semiarboreal forms included in the present study have been cited in an earlier part of this paper. Records of the arboreal behavior of certain other forms of peromyscus are also available. Cahalane (1939: 433) reported that several Peromyscus boyli rowleyi which "escaped while being transferred from traps to cages fled into trees in preference to running on the ground." This habit of taking refuge in trees had earlier been noted by Dice, who observed the progression of rowleyi mice from tree to tree by way of interlacing branches and was able to photograph one in an oak tree into which it had climbed (Dice and Blossom, 1937: 36, Pl. 2). The tree nests of three subspecies of Peromyscus nuttalli have been described by several authors (Pickens, 1927: 246-47; Welter and Sollberger, 1939: 80-81; Lewis, 1940: 427; Barbour, 1942: 90-91; Moore, 1946: 57). There is no doubt, therefore, that scansorial activity plays an important role in the lives of many of the forms of the genus Peromyscus.

Even though they may nest in trees or climb trees in search of food or to escape from predators, the most arboreally inclined of the peromyscan forms are at home on the ground. Results of the present study, together with previously reported experimental work, indicate that in peromyscus semiarborealness is distinguished from terrestrialness in some highly complex manner. Clark (1936) found that three semiarboreal and three terrestrial forms differed in geotropic behavior. Mice of the semiarboreal group studied by him were more sensitive to slight inclinations and responded by traveling along higher orientation angles to slopes than did mice of the terrestrial group. More recently Harris (1952), working with the semiarboreal gracilis and the terrestrial bairdi, demonstrated that each of these tends to select an artificial habitat which simulates its natural one. In the present study a diversified group of peromyscan forms showed a correlation in tail length, climbing ability, and reaction to elevation with natural habit. Additional information offered by this and the two studies cited above makes clear that the terrestrial forms all exhibited to at least some degree whatever feature is of particular adaptive value to the forms of scansorial habits. The semiarboreal forms, it is true, are better adapted for scansorial existence than are the terrestrial ones, but there remains the question of why the forms classed as terrestrial do virtually no climbing under natural undisturbed conditions, as seems to be the case. All terrestrial peromyscus live in places characterized by some form of climbable vegetation, sparse though it may be. All of the forms studied here were perfectly able to climb and showed no marked aversion to climbing under laboratory conditions. Certainly, the complex of factors influencing the climbing behavior of peromyscus is still little understood, and much additional study is required before the subtleties of the relationship between habit and habitat can be fully explained.

In comparing the climbing ability of peromyscus with that of other mammals, it is evident that even the most arboreal peromyscus are less arboreal than are such forms as, for example, the sloth, the gibbon, and the tree squirrels. The tree squirrels, such as Glaucomys, Tamiasciurus, and Sciurus, represent a category which includes those animals which travel along the upper surfaces of branches by means of all four limbs. To this group, that contains the majority of arboreally inclined mammals, belongs peromyscus, which has evolved according to the general pattern of arboreal adaptation rather than according to the unique pattern of either the sloth or the gibbon.

Among the mammals with adaptations for arboreal locomotion are many forms besides peromyscus in which the tail plays an important role in progression, and in several closely related forms tail length varies directly with arborealness. Although the native microtines are, in general, terrestrial, fossorial, or semiaquatic, there are two species of Phenacomys, longicaudus and silvicola, which, because of their largely arboreal habits are known as tree mice. In each of these two species the average tail length is both absolutely and relatively greater than is that of any of the other four species recognized (measurements from Howell, 1926). In the genus Sciurus, the gray squirrel (S. carolinensis), which is a more agile climber than is the fox squirrel (S. niger rufiventer), has a relatively longer tail (see measurements given by Burt 1946). A similar condition exists among murine rats; Rattus rattus is a more skillful climber and has a relatively longer tail than R. norvegicus (see measurements given by Anthony, 1928, and Cahalane, 1947). Likewise, the fisher (Martes pennanti), which is so swift in its arboreal progression as to be able to overtake the marten (M. americana), has a relatively longer tail (see Burt, 1946, and Cahalane, 1947). Although exceptions may occur, the correlation between relative tail length and the climbing proficiency of closely related mammals which run along branches seems to be of fairly universal occurrence.

Not all long-tailed mammals are arboreal, however, nor are all arboreal mammals long-tailed. In the kangaroo rat (Dipodomys) and the jumping mouse (Zapus), the remarkably long tail serves as an equilibrator in adaptation to the leaping habits (Hatt, 1932; Howell, 1932); and the fairly long, laterally compressed tail of the muskrat (Ondatra), on the other hand, acts as a rudder (Cahalane, 1947: 525). Among the several short-tailed mammals which are at home in the trees may be mentioned the sloth (Choloepus and Bradypus) and the gibbon (Hylobates). The balancing function of a tail would be of little use to an upside-down traveler such as the sloth, and special adaptation for long periods of suspension from the branches is gained by marked modifications of the appendages (Britton, 1941) rather than by the development of a long prehensile tail like that of the opossum and certain of the monkeys. The virtually tailless gibbons are primarily brachiators, swinging by their long arms from branch to branch with ease and speed. Where the maintenance of balance is required, as is the case when these animals walk or run along branches, the tremendously elongated arms are held high or extended to the sides and very obviously used as balancing organs (Carpenter, 1940), thus having a function comparable to that of the long tails of certain mammals which use all four of their appendages in running along branches. These are but a few illustrations which indicate not only that a long tail may serve functions other than those concerned with arboreal locomotion, but that arboreal habits are not necessarily dependent upon the development of a long tail.

The differences distinguishing the higher taxonomic categories are generally held to be the result of adaptation. There has been some question, however, as to the adaptive value of the ones used as criteria to distinguish the lower categories. Especially has considerable doubt been expressed from time to time regarding the adaptive value of subspecific differences. That subspecific characters in peromyscus are inherited was first proved by Sumner (1932: 28-30), and it has been confirmed by many later studies. The adaptive value of one of these subspecific characters, that of pelage color, was brought out by the experiments of Dice (1947). The results of the present study demonstrate the adaptive value of another subspecific character, that of tail length. In the wide-ranging genus Peromyscus, therefore, the characters used to differentiate subspecies are not only inherited but, at least in these two instances, are also adaptive.

SUMMARY

A laboratory investigation was made of the climbing behavior and ability of mice of ten forms of the genus Peromyscus. Six of the forms are subspecies of the species maniculatus. Peromyscus maniculatus gracilis, P.m. oreas, P. leucopus noveboracensis, P. nasutus nasutus, and P. truei truei are semiarboreal in their natural habitats; P.m. bairdi, P.m. blandus, P.m. nebrascensis, and P. polionotus leucocephalus live in grasslands or in beach or desert country where trees are relatively infrequent. The stock of P.m. rubidus originated near Hood River, Oregon, at the edge of the coastal forest. The semiarboreal forms differ from the terrestrial forms, in general, in that the tails and hind feet are both absolutely and relatively longer as compared with body length.

Mice of all of the forms climbed to elevated levels when the experimental apparatus offered was sufficiently easy to climb and when the animals were allowed time to explore freely.

In reaction to high places, the semiarboreal forms showed a significantly greater tendency than did those of the terrestrial forms to remain on an elevated platform in the absence of a pathway to the ground. Whether on elevated branches or platforms the semiarboreal mice were also less nervous and more aware of the general relationship to the ground than were the terrestrial.

In vertical climbing, natural tree trunks of moderate roughness were easily climbed by mice of all of the forms, but members of the terrestrial forms exhibited significantly greater difficulty in climbing a trunk of relatively smooth-, hard-barked surface, such as that of the beech (Fagus), than did those of the semiarboreal. Each of the five semiarboreal forms differed significantly from each of the four terrestrial forms in greater ability to climb artificial trunks of several different diameters and grades of smoothness.

In crossing gaps, mice of the semiarboreal forms were able to reach and to jump greater distances than were those of the terrestrial forms. Spontaneous jumping from branch to branch, however, was infrequent.

In climbing horizontally along tubes, roughened and otherwise simulating small branches, the semiarboreal forms exhibited greater proficiency, in general, than the terrestrial. With the single exception of nasutus, each of the semiarboreal forms showed a significantly greater ability, as measured by mean number of performance errors, in traveling along such branches than did any of the terrestrial forms.

Amputation of the tail seriously handicapped the arboreal proficiency of the mice, but the resultant handicap was greater for the long-tailed than for the short-tailed forms. The long tail of the semiarboreal forms of the genus Peromyscus is thus demonstrated to be an adaptive structure which facilitates an existence in semiarboreal habitats. A marked advantage shown by the long tail over the short tail is its greater effectiveness as a balancing organ. The long tail is also more effective than the short tail in prehension, as a tactile organ, and as a prop.

The semiarboreal forms are, as a whole, better adapted for climbing than the terrestrial forms, not only by virtue of their relatively longer

tails, but also because they show less nervousness on elevated branches and greater awareness of the general relationship of their elevated supports to the ground. The climbing performance of rubidus, the stock from a type of habitat intermediate between forest and open field, sometimes was aligned with the performance of the semiarboreal forms and sometimes fell between that of the semiarboreal and that of the terrestrial groups. In mice of the genus Peromyscus, therefore, the results of these experiments bear out that adaptation for arboreal life involves modification of both body proportions and behavior.

LITERATURE CITED

ALLEN, DURWARD L.

1943 Michigan fox squirrel management. Lansing, Mich.: Dept. Conserv., Game Div. Publ., No. 100: 1-404.

ANTHONY, H. E.

1928 Field book of North American mammals. New York: G. P. Putnam's Sons.

BAILEY, VERNON

1931 Mammals of New Mexico. U.S. Dept. Agric., Bur. Biol. Surv., N. Amer. Fauna, 53: 1-412.

BARBOUR, ROGER W.

1942 Nest and habitat of the golden mouse in eastern Kentucky. Journ. Mammal., 23: 90-91.

BEHNEY, W. H.

1936 Nocturnal explorations of the forest deer-mouse. Journ. Mammal., 17: 225-30.

BLAIR, W. FRANK

1940 A study of prairie deer-mouse populations in southern Michigan. Amer. Midl. Nat., 24: 273-305.

1941 Annotated list of mammals of the Tularosa Basin, New Mexico. Ibid., 26: 218-29.

1943 Activities of the Ghihuahua deer-mouse in relation to light intensity. Journ. Wildlife Management, 7: 92-97.

1951 Population structure, social behavior, and environmental relations in a natural population of the beach mouse (Peromyscus polionotus leucocephalus). Contrib. Lab. Vert. Biol. Univ. Mich., 48: 1-47.

BRITTON, S. W.

1941 Form and function in the sloth. Quart. Rev. Biol., 16: 13-34, 190-20.

BUCK, C. W., N. TOLMAN, and W. TOLMAN

1925 The tail as a balancing organ in mice. Journ. Mammal., 6: 267-71.

BURT, WILLIAM HENRY

1940 Territorial behavior and populations of some small mammals in southern Michigan. Misc. Publ. Mus. Zool. Univ. Mich., 45: 1-58.

1946 The mammals of Michigan. Ann Arbor: Univ. Mich. Press.

CAHALANE, VICTOR H.

1939 Mammals of the Chiricahua Mountains, Cochise County, Arizona. Journ. Mammal., 20: 418-40.

1947 Mammals of North America. New York: The Macmillan Co.

CARPENTER, C. R.

1940 A field study in Siam of the behavior and social relations of the gibbon (Hylobates lar), with introduction by A. H. Schultz. Comp. Psychol. Monog., 16: 1-212.

CLARK, FRANK H.

1936 Geotropic behavior on a sloping plane of arboreal and non-arboreal races of mice of the genus Peromyscus. Journ. Mammal., 17: 44-47.

1941 Correlation and body proportions in mature mice of the genus Peromyscus. Genetics, 26: 283-300.

DALQUEST, WALTER W.

1948 Mammals of Washington. Univ. Kans. Publ. Mus. Nat. Hist., 2: 1-444.

DICE, LEE R.

1925a A Survey of the mammals of Charlevoix County, Michigan, and vicinity. Occ. Papers Mus. Zool. Univ. Mich., 159: 1-33.

1925b The mammals of Marion Island, Grand Traverse County, Michigan. Ibid., 160: 1-8.

1929 A new laboratory cage for small mammals with notes on methods of rearing Peromyscus. Journ. Mammal., 10: 116-124.

1930 Mammal distribution in the Alamogordo region, New Mexico. Occ. Papers Mus. Zool. Univ. Mich., 213: 1-32.

1932 Variation in a geographic race of the deer-mouse, Peromyscus maniculatus bairdii. Ibid., 239: 1-26.

1937 Variation in the wood-mouse, Peromyscus leucopus noveboracensis, in the northeastern United States. Ibid., 352: 1-32.

1940 Ecologic and genetic variability within species of Peromyscus. Amer. Nat., 74: 212-21.

1941a Variation of the deer-mouse (Peromyscus maniculatus) on the sand hills of Nebraska and adjacent areas. Contrib. Lab. Vert. Gen. Univ. Mich., 15: 1-19.

1941b Variation in the deer-mouse, Peromyscus maniculatus, in parts of Oregon, California, and Baja California. Ibid., 18: 1-11.

1942 Ecological distribution of Peromyscus and Neotoma in parts of southern New Mexico. Ecology, 23: 199-208.

1947 Effectiveness of selection by owls of deer-mice (Peromyscus maniculatus) which contrast in color with their background. Contrib. Lab. Vert. Biol. Univ. Mich., 34: 1-20.

1949 Variation of Peromyscus maniculatus in parts of western Washington and adjacent Oregon. Ibid., 44: 1-34.

DICE, LEE R., and PHILIP M. BLOSSOM

1937 Studies of mammalian ecology in southwestern North America with special attention to the colors of desert mammals. Carnegie Instit. Wash., Publ. No. 485: 1-125.

DICE, LEE R., and H. B. SHERMAN

1922 Notes on the mammals of Gogebic and Ontonagon Counties, Michigan, 1920. Occ. Papers Mus. Zool. Univ. Mich., 109: 1-46.

DOR, M.

1937 La morphologie de la queue des mammifères dans ses rapports avec la locomotion. Paris: Pierre André.

GRIFFIN, DONALD R.

1944 Echolocation by blind men, bats and radar. Science, 100: 589-90.

HAMILTON, WILLIAM J., JR.

1928 The height from which rodents may fall. Journ. Mammal., 9: 65-66.

HARRIS, VAN T.

1952 An experimental study of habitat selection by prairie and forest races of the deermouse, Peromyscus maniculatus. Contrib. Lab. Vert. Biol. Univ. Mich., 56: 1-53.

HATT, ROBERT T.

1932 The vertebral columns of ricochetal rodents. Bull. Amer. Mus. Nat. Hist., 63: 599-738.

HAYNE, DON W.

1950 Reliability of laboratory-bred stocks as samples of wild populations, as shown in a study of the variation of Peromyscus polionotus in parts of Florida and Alabama. Contrib. Lab. Vert. Biol. Univ. Mich., 46: 1-56.

HOFFMEISTER, DONALD F.

1951 A taxonomic and evolutionary study of the piñon mouse, Peromyscus truei. Illinois Biol. Monogr., 21, No. 4: 1-104.

HORNER, B. ELIZABETH

1947 Paternal care of young mice of the genus Peromyscus. Journ. Mammal., 28: 31-36.

HOWARD, WALTER E.

1949 Dispersal, amount of inbreeding, and longevity in a local population of prairie deermice on the George Reserve, southern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 43: 1-50.

HOWELL, A. BRAZIER

1926 Voles of the genus Phenacomys. U.S. Dept. Agric., Bur. Biol. Surv., N. Amer. Fauna, 48: 1-66.

1932 The saltatorial rodent Dipodomys: the functional and comparative anatomy of its muscular and osseous systems. Proc. Amer. Acad. Arts and Sci., 67: 377-536.

HOWELL, ARTHUR H.

1920 Description of a new species of beach mouse from Florida. Journ. Mammal., 1: 237-240.

JOHNSON, CHARLES EUGENE

1922 Notes on the mammals of northern Lake County, Minnesota. Journ. Mammal., 3: 33-39.

JOHNSON, M. S.

1926 Activity and distribution of certain wild mice in relation to biotic communities. Journ. Mammal., 7: 245-77.

LEWIS, JOHN B.

1940 Mammals of Amelia County, Virginia. Journ. Mammal., 21: 422-28.

LÖHRL, HANS

1938 Ökologische und physiologische Studien an einheimischen Muriden und Soriciden. Zeitschr. f. Saugetierkunde, 13: 114-60.

MANVILLE, RICHARD H.

1949 A study of small mammal populations in northern Michigan. Misc. Publ. Mus. Zool. Univ. Mich., 73: 1-83.

McCABE, THOMAS T., and BARBARA D. BLANCHARD

1950 Three species of Peromyscus. Santa Barbara, Calif.: Rood Associates.

MOORE, JOSEPH C.

1946 Mammals from Welaka, Putnam County, Florida. Journ. Mammal., 27: 49-59.

MURIE, ADOLPH

1933 The ecological relationship of two subspecies of Peromyscus in the Glacier Park region, Montana. Occ. Papers Mus. Zool. Univ. Mich., 270: 1-17.

NELSON, EDWARD W.

1918 Wild Animals of North America. Washington, D.C.: National Geographic Society.

NICHOLSON, ARNOLD J.

1941 The homes and social habits of the wood-mouse (Peromyscus leucopus noveboracensis) in southern Michigan. Amer. Midl. Nat., 25: 196-223.

OSGOOD, WILFRED H.

1909 A revision of the mice of the American genus Peromyscus. U.S. Dept. Agric., Bur. Biol. Surv., N. Amer. Fauna, 28: 1-285.

PICKENS, ANDREW L.

1927 Golden mice in upper South Carolina. Journ. Mammal., 8: 246-48.

SHUFELDT, R. W.

1885 Description of Hesperomys truei, a new species belonging to the subfamily Murinae. Proc. U.S. Nat. Mus., 8: 403-8.

SUMNER, F. B.

1926 An analysis of geographic variation in mice of the Peromyscus polionotus group from Florida and Alabama. Journ. Mammal., 7: 149-84.

1932 Genetic, distributional, and evolutionary studies of the subspecies of deer mice (Peromyscus). Biblio. Genetica, 9: 1-106.

SVIHLA, ARTHUR

1932 A comparative life history study of the mice of the genus Peromyscus. Misc. Publ. Mus. Zool. Univ. Mich., 24: 1-39.

1933 Notes on the deer-mouse, Peromyscus maniculatus oreas (Bangs). Murrelet, 14: 13-14.

WELTER, WILFRED A., and DWIGHT E. SOLLBERGER

1939 Notes on the mammals of Rowan and adjacent counties in eastern Kentucky. Journ. Mammal., 20: 77-81.

WHITAKER, WAYNE L.

1940 Some effects of artificial illumination on reproduction in the white-footed mouse, Peromyscus leucopus noveboracensis. Journ. Exper. Zool., 83: 33-60.

Department of Zoology
Smith College
Northampton, Mass.

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price $1.25.

PLATE I

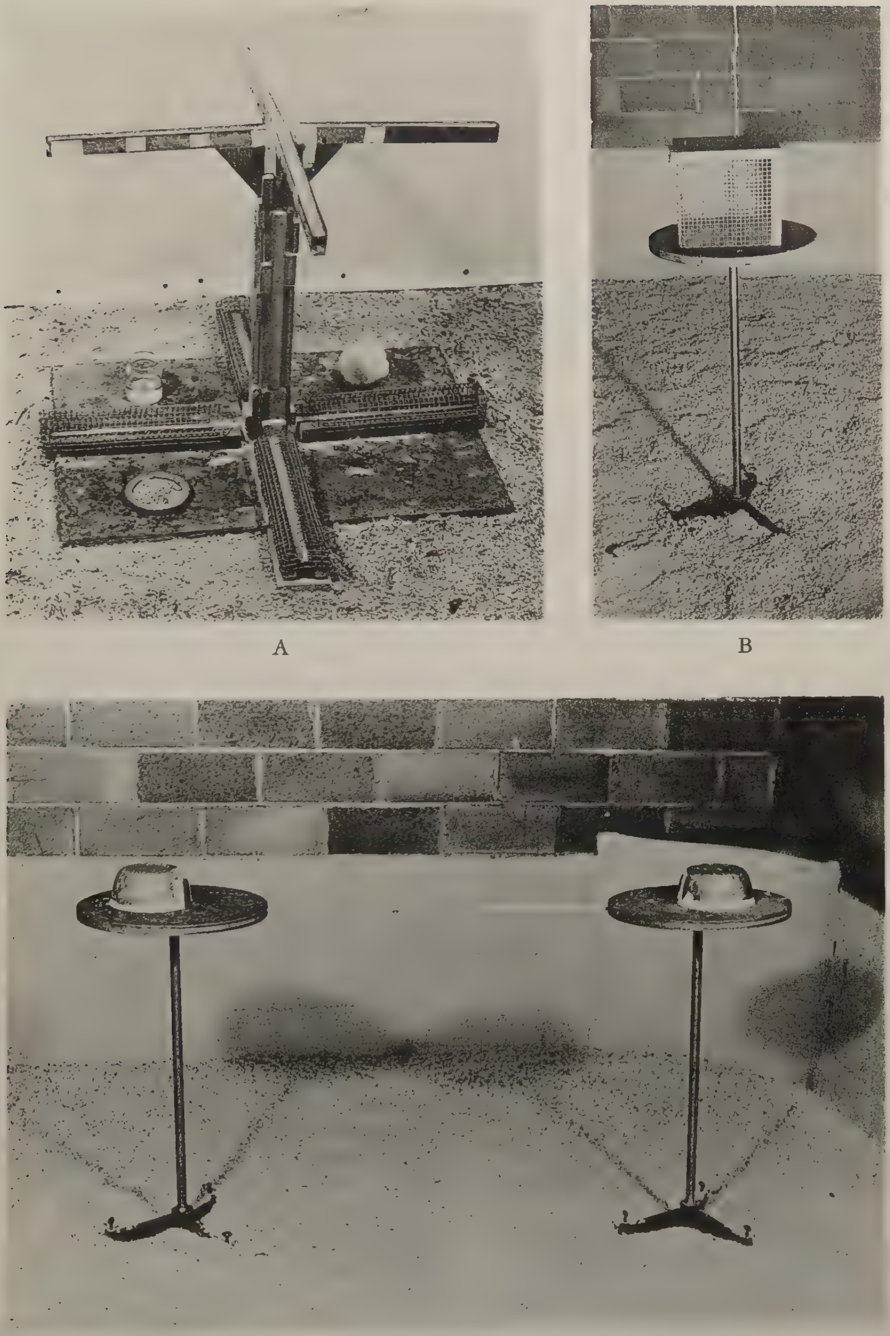
Equipment

Fig. A. Apparatus for study of the reaction of peromyscus to the climbing of easily climbed objects.

Fig. B. Platform and cage used in study of the reaction of mice to elevation.

Fig. C. Apparatus employed in measuring the tube-crossing proficiency of the mice.

PLATE I

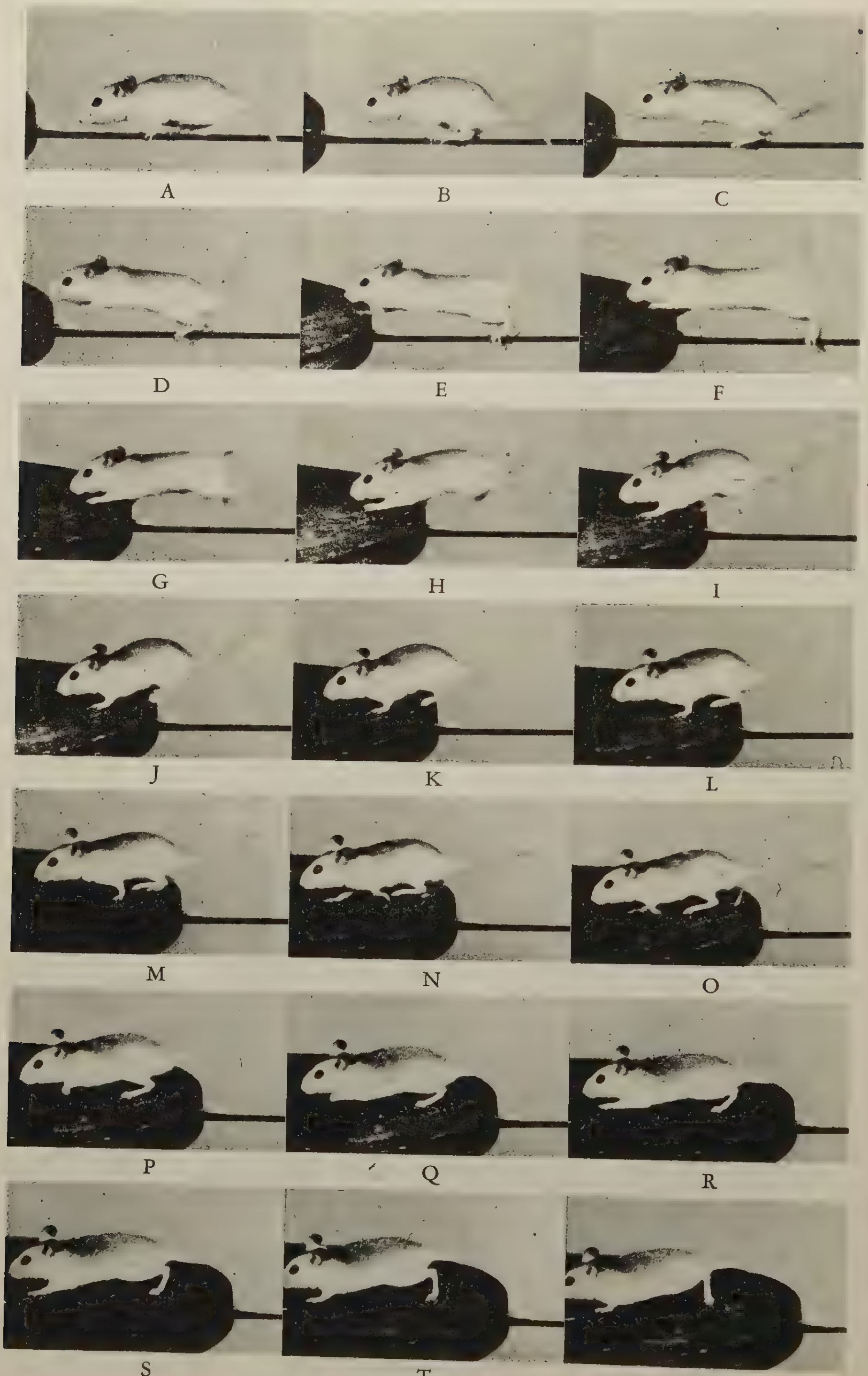


A

B

C

PLATE II



A B C D E F G H I J K L M N O P Q R S T U

PLATE II

Climbing Movements of Peromyscus

Motion-picture records; photographs enlarged from 16-millimeter film, 64 exposures per second.

Figs. A-U. Peromyscus polionotus leucocephalus bounding from a tube of 3 mm. in diameter onto a platform and walking across the platform. The fore feet left the tube almost simultaneously as later did the hind feet. For a fraction of a second the body of the mouse was unsupported (G, and possibly H). In landing on the platform, the mouse placed its feet in the following order: right fore, left fore, right hind, and left hind, the left hind foot retaining contact with the platform only momentarily. In walking forward on the platform, the mouse placed its feet individually in a characteristic walking order: right fore, left hind, left fore, and right hind. (21 consecutive frames.)

PLATE III

Climbing Movements of Peromyscus

Motion-picture records; photographs enlarged from 16-millimeter film, 64 exposures per second.

Figs. A-D. Peromyscus maniculatus blandus ascending a sloping branch (Lonicera). The tail was raised and moved rapidly as balance became difficult and was flexed under the branch as the mouse began to slip. (Interrupted sequence of frames.)

Figs. E-L. Same blandus mouse descending from one branch to another. The relatively short tail left the upper branch shortly after release of the hind feet and the mouse slipped in landing on the lower branch. Immediately after recovery from slipping the tail was used to maintain balance. (Interrupted sequence of frames.)

Figs. M-P. Peromyscus nasutus nasutus descending a tree trunk (Acer negundo). The tail was held close to but not pressed against the trunk. The feet were placed individually and the degree of rotation of the hind limbs was less than that frequently observed in tree squirrels. (Interrupted sequence of frames.)

Figs. Q-T. Same nasutus ascending the same tree trunk. The tail was held close to the trunk but not pressed against it. The feet were moved individually. (Interrupted sequence of frames.)

Figs. U-X. Peromyscus polionotus leucocephalus ascending the same Acer negundo trunk. The locomotion of the mouse, which moved the hind legs together, illustrates a mode of ascent occasionally employed by peromyscus, but far more frequently by the tree squirrels. (4 consecutive frames.)

PLATE III

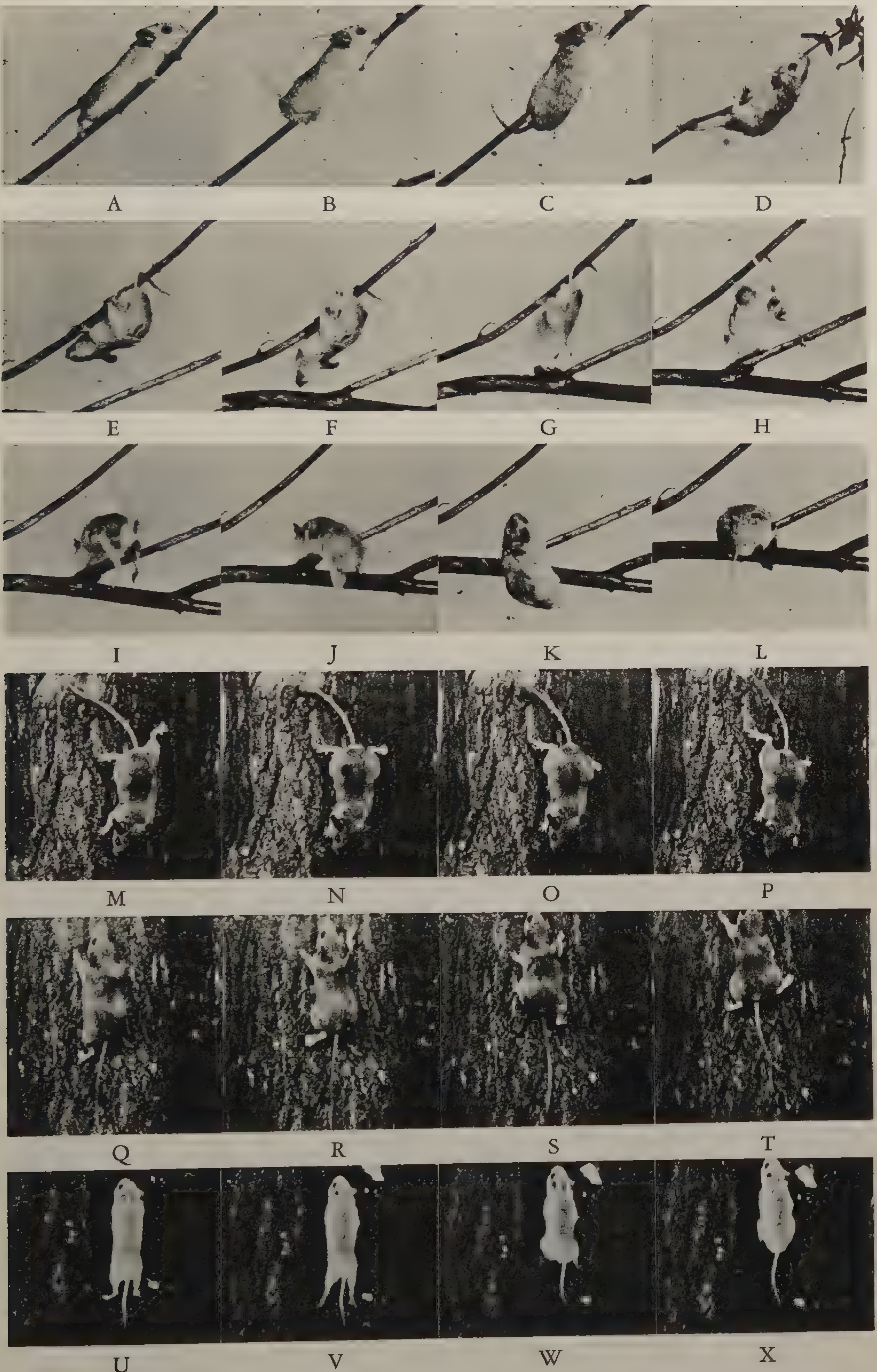


PLATE IV

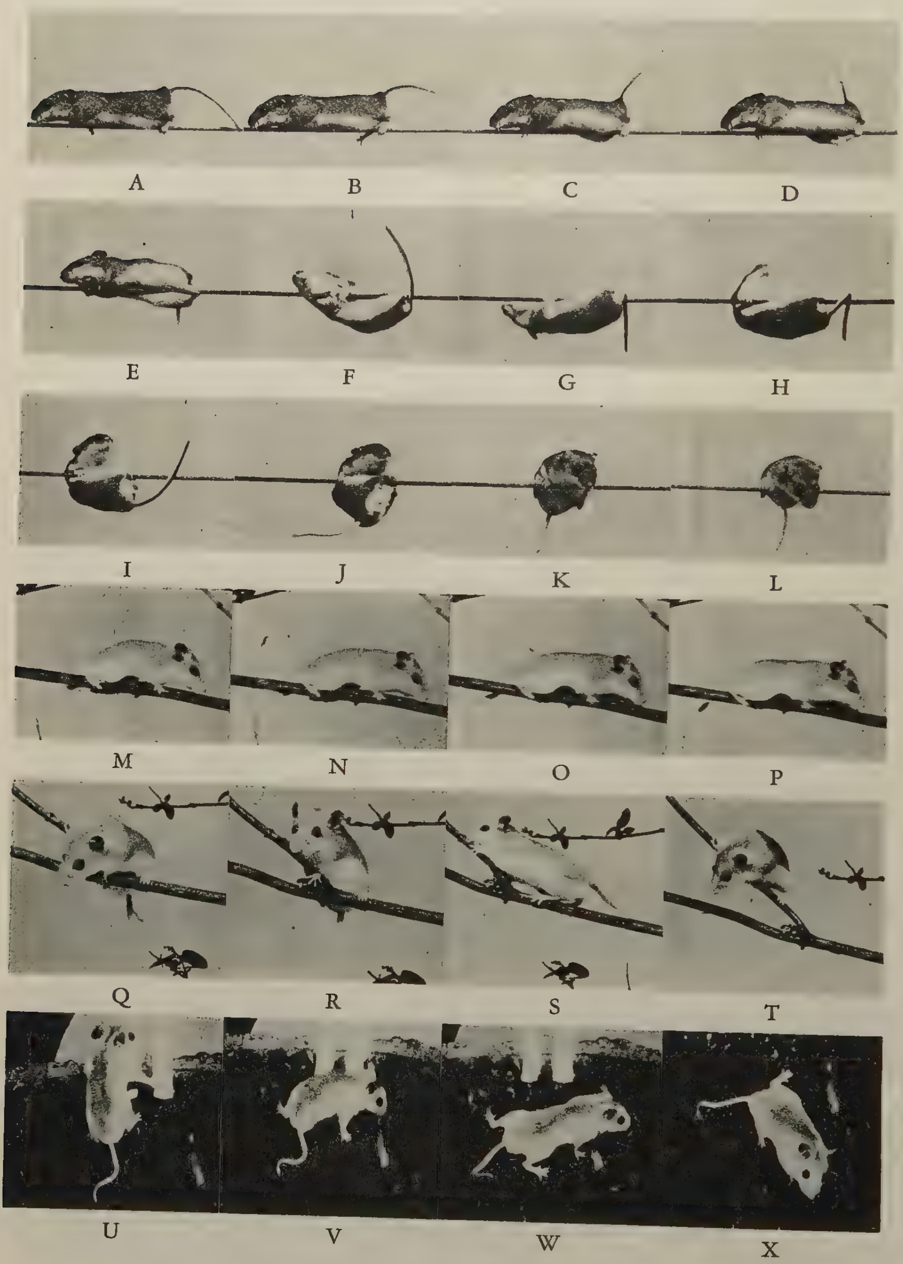


PLATE IV

Climbing Movements of Peromyscus

Motion-picture records; photographs enlarged from 16-millimeter film, 64 exposures per second.

Figs. A-D. Peromyscus maniculatus bairdi crossing a roughened tube of 3 mm. in diameter. Slipping of the right hind foot from the tube was not followed by slipping of the body below the tube. Balancing movements of the tail were evident. (4 consecutive frames.)

Figs. E-L. Same bairdi mouse slipping below the tube. Note use of the feet and tail in recovery of mouse from inverted position. (Interrupted sequence of frames.)

Figs. M-P. Peromyscus maniculatus nebrascensis flexing the proximal part of its tail under a branch and then gradually releasing its tail hold on the branch as loss of balance becomes less imminent. (4 consecutive frames.)

Figs. Q-T. Same nebrascensis mouse showing the placement of its toes. The spreading of the toes of the left fore foot is evident (Q, R, and S). In S the hind toes are also widely separated. In Q, R, and T, where the mouse is sitting crosswise on the branch, the toes of the visible hind foot are held closer together. (Interrupted sequence of frames.)

Figs. U-X. Peromyscus polionotus leucocephalus using its tail as a prop (U and V), as a combined prop and prehensile organ (W), and as a prehensile organ only (X). The mouse was turning about near the top of a section of tree trunk (Acer negundo). The tail was braced against a projecting piece of bark as the front feet of the mouse encountered and then turned away from a smooth-surfaced obstacle at the top of the trunk. In turning downward the mouse used its tail progressively less as a prop and progressively more as a prehensile organ. (Interrupted sequence of frames.)

PLATE V

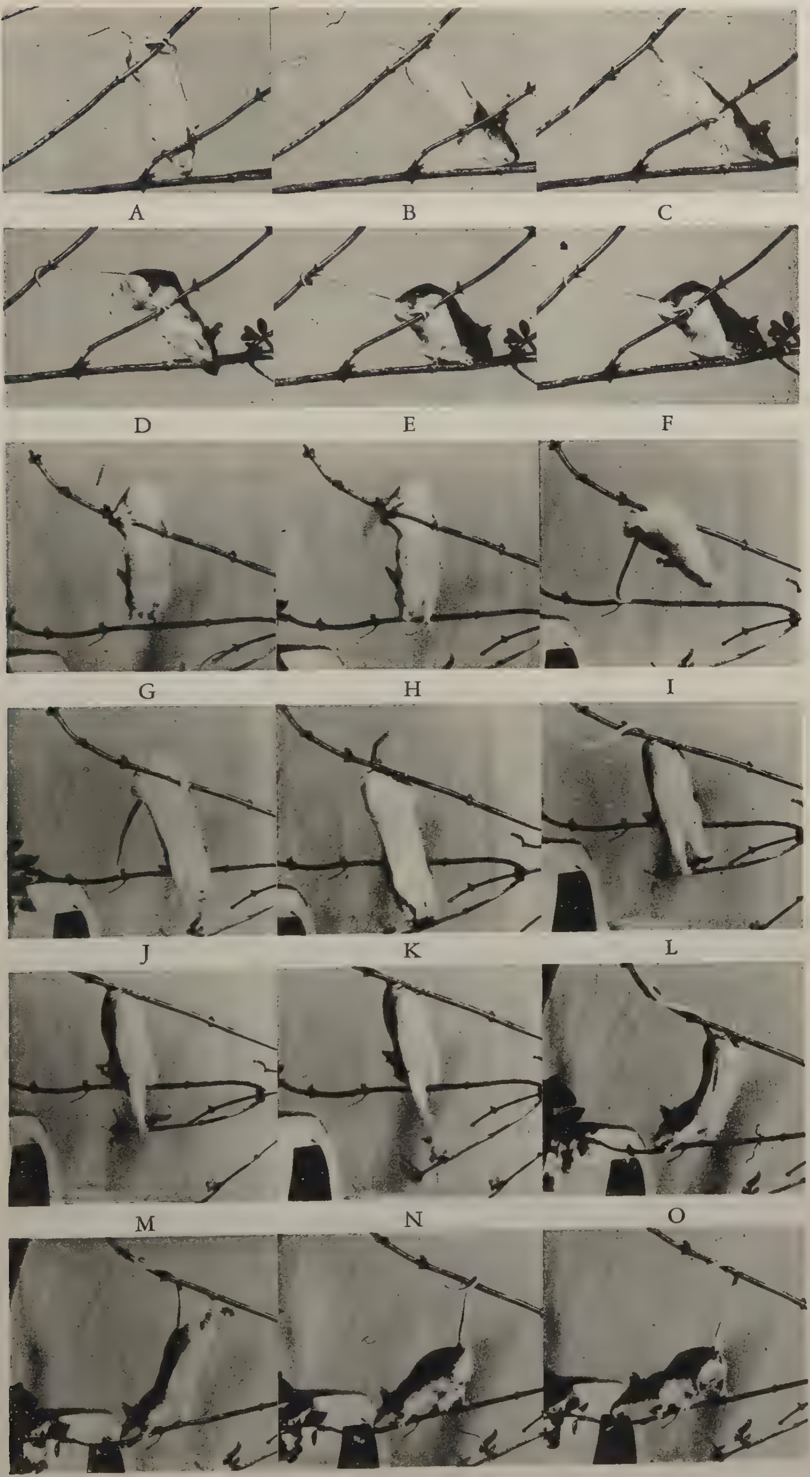
Climbing Movements of Peromyscus

Motion-picture records; photographs enlarged from 16-millimeter film, 64 exposures per second.

Figs. A-F. Peromyscus leucopus noveboracensis making a successful descent from one to another of two somewhat flexible branches (Lonicera). The tail in maintaining its hold on the upper branch all the while that the hind feet were being lowered to the other branch, retarded the rate of falling of the hind quarters of the mouse and thereby facilitated accurate placement of the hind feet on the lower branch. (Interrupted sequence of frames.)

Figs. G-R. Same noveboracensis mouse, having attempted to reach down to the branch leading to the igloo, reaches down to the shorter branch in the foreground. This branch, together with the longer branch, was then pulled closer to the upper branch by the mouse. The animal next reached over to the longer branch, onto which it lowered the rest of its body. The tail was used to retard the rate of falling of the hind quarters. The flexibility of the branches, particularly of the lower ones, is apparent from their very noticeable bending under the weight of the mouse. (Interrupted sequence of frames.)

PLATE V



A B C

D E F

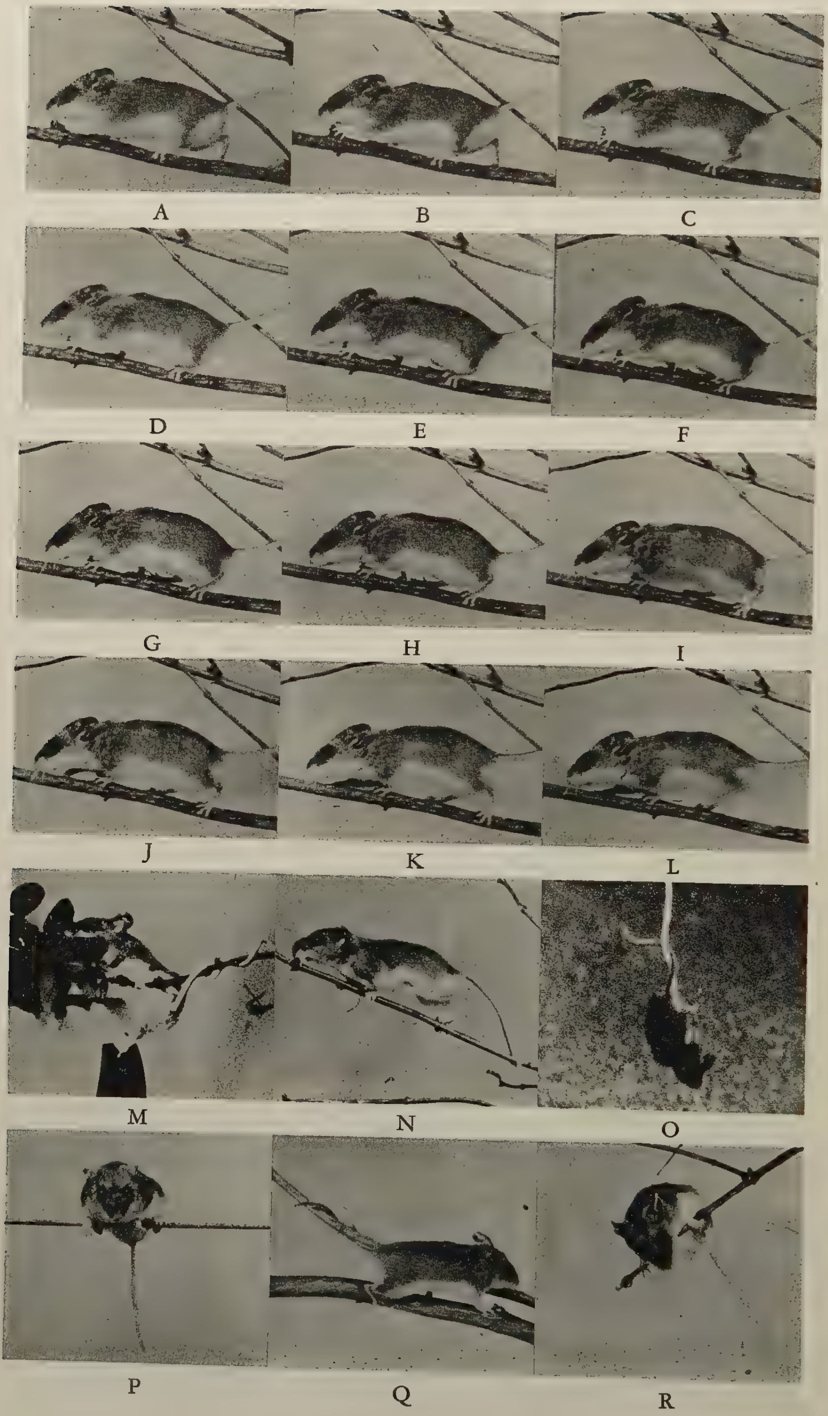
G H I

J K L

M N O

P Q R

PLATE VI



A B C

D E F

G H I

J K L

M N O

P Q R

PLATE VI

Climbing Movements of Peromyscus

Motion-picture records; photographs enlarged from 16-millimeter film, 64 exposures per second.

Figs. A-L. Peromyscus maniculatus gracilis traveling along a branch. Note the spreading of the toes of both the fore and hind feet. The order in which the feet were raised is as follows: left fore, right hind, right fore, and left hind. (12 consecutive frames.)

Fig. M. Peromyscus leucopus noveboracensis using its prehensile tail in recovering its upright position on a flexible branch.

Fig. N. Same noveboracensis mouse progressing along a branch with the tip of its tail flexed loosely below that branch.

Fig. O. Peromyscus maniculatus gracilis flexing its tail around a cord in such a manner as to decrease the rate of descent.

Fig. P. Peromyscus maniculatus bairdi sitting crosswise on a tube 3 mm. in diameter. The toes of the hind feet grasped the tube and the fore legs rested on the tube. The fore feet were not in contact with the support.

Fig. Q. Peromyscus maniculatus gracilis showing prehensile use of the tail as the animal progressed from one to another of two nearby branches.

Fig. R. Same gracilis mouse sitting crosswise near the end of a flexible branch in a position similar to that of bairdi (Fig. P). The tails of both of these mice are straight and taut and are of great importance in the maintenance of these sitting positions.

PLATE VII

Climbing Movements of Peromyscus

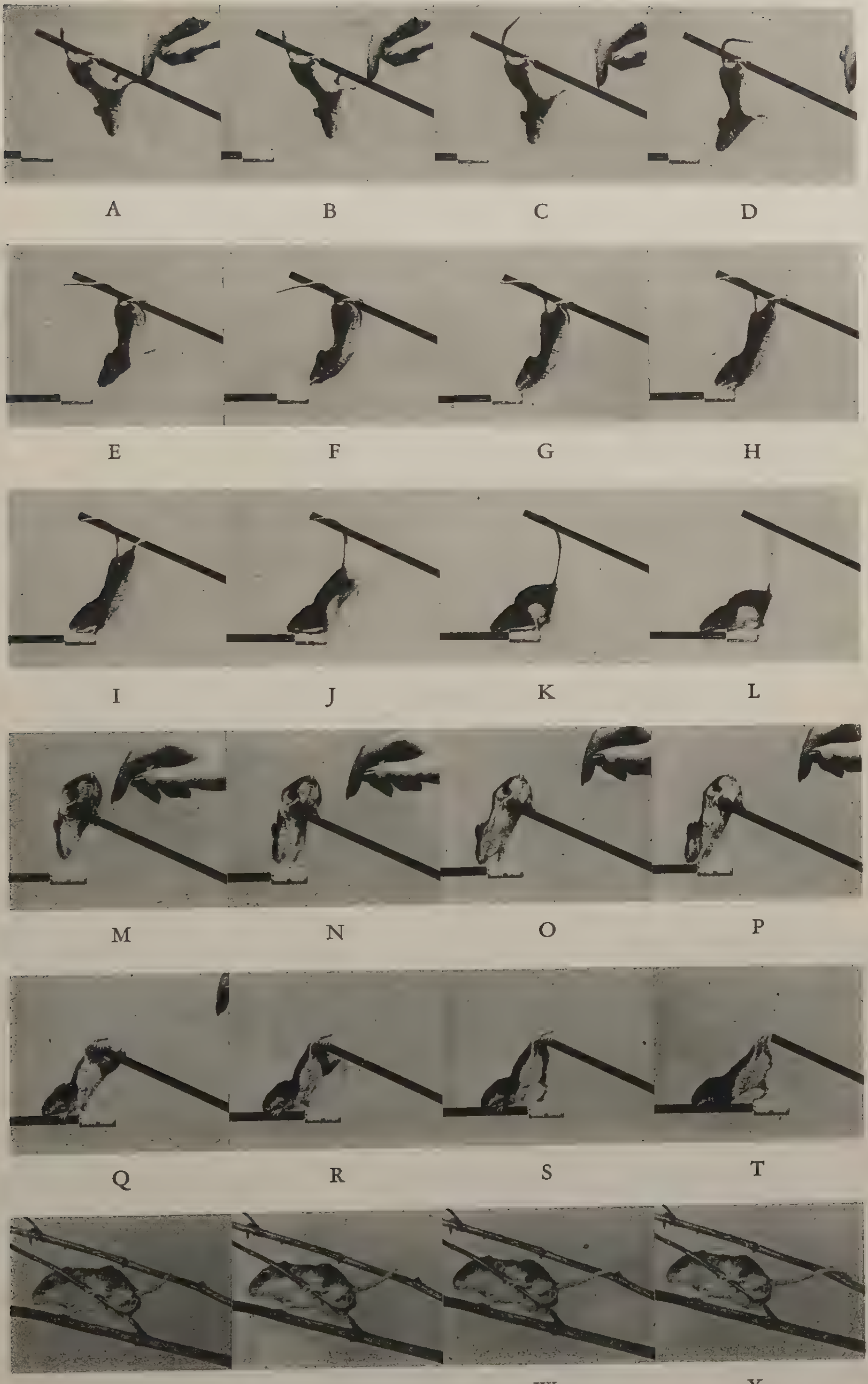
Motion-picture records; photographs enlarged from 16-millimeter film, 64 exposures per second.

Figs. A-L. Peromyscus maniculatus gracilis spanning a gap of 10.5 cm. in reaching downward from one tube to another. The tail was flexed over the upper tube both before and after the hind feet were released. The front feet were placed almost simultaneously on the lower tube as later were the hind feet. (Nonconsecutive frames for the most part.)

Figs. M-T. A tailless gracilis mouse spanning a gap of approximately 5 cm. in reaching downward. The feet were placed individually on the lower tube, the two hind feet following the two fore feet. (Interrupted sequence of frames.)

Figs. U-X. Peromyscus truei truei using its tail as a balancing organ (U and V) and then flexing it over (X) a branch which has been touched (W).

PLATE VII



A B C D

E F G H

I J K L

M N O P

Q R S T

U V W X

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

University of Michigan, Ann Arbor, Michigan

Number 62 February, 1953

THE STATISTICAL CONCEPT OF HOME RANGE AS APPLIED TO THE RECAPTURE RADIUS OF THE DEERMOUSE (PEROMYSCUS)

By LEE R. DICE and PHILIP J. CLARK

Accepted for publication October 7, 1952

CONTENTS

Introduction 1
General Considerations 2
Statistical Treatment of Recapture Radii 2
Application to Trapping Records of the Deermouse 6
Relation of Certain Factors to Recapture Radius 11
Summary 13
Literature Cited 14

INTRODUCTION

A KNOWLEDGE of the area occupied by an individual animal in a population is of high ecologic interest. The area occupied affects population density, competition between individuals, reproductive success, utilization of food and other resources, social organization, relations between species, and other features of community dynamics.

In recent years numerous studies have been made of the home ranges of certain kinds of animals, and various methods have been developed for measuring home-range area (Burt, 1940; Blair, 1940; Dice, 1951; Haugen, 1942; Hayne, 1949). Most of these methods have assumed a more or less rigid boundary for each home range. It is recognized that an individual may sometimes be found at a considerable distance outside its usual home range, but it is almost impossible to decide which records are "unusual" and which are regular. The statistical treatment of the records has consequently been difficult.

To replace the idea that each home range has a fixed boundary, if only this boundary could be ascertained, Hayne (1949) has introduced the concept of a "center of activity" and has considered the probability of capturing an animal at various distances from this center. In general, the greater the distance from the center of activity, the lower is the probability of capturing the animal. Aside from the presence of physical barriers, however, there exists no boundary beyond which a given animal may not pass. If an animal has no fixed limits to its wanderings, the attempt to ascertain home-range boundaries or home-range areas is futile.

We here utilize Hayne's concept of home range, and we extend this concept by suggesting a more precise and a more general method for estimating the probability associated with any specified distance from the center of activity.

We are jointly responsible for developing the concepts here used and have collaborated in writing the paper. We are indebted to Professor C. C. Craig, of the University of Michigan's Statistical Research Laboratory, for critically reading the manuscript.

GENERAL CONSIDERATIONS

As an animal travels over its home area it occupies an infinite number of positions, which may be called "activity loci." For any given period of time there exists for these loci (in two-dimensional Cartesian space) a geometric center, the "center of activity" of that animal. The distance between an activity locus and the center of activity may be called the "activity radius." In order to estimate the probability that an activity radius taken at random for a given individual will exceed a certain value, it is necessary to have a random sample of that individual's activity loci.

The activity loci successively occupied by a diurnal animal in its movements over its home range can often be ascertained by direct observation. A random sample of its activity loci can consequently be obtained by recording its position at random instants of time. Records of activity loci taken at regularly spaced instants, however, should give a sufficiently close approach to a random sample for all practical purposes, providing the various loci are essentially independent of one another.

STATISTICAL TREATMENT OF RECAPTURE RADII

For many species of animals it is impractical to ascertain the activity loci in any way other than by the retrapping of marked individuals. For securing information about the movements of such animals a grid of traps may be extended over an area sufficiently large to include all the activity loci of at least one individual. The presence of the traps, however, modifies the movements of the animals to some extent, so that the activity loci and the center of activity ascertained from trapping records may not be fully descriptive of the movements over its home range of an uninhibited animal.

The following discussion will be restricted to a consideration of the distance between a given recapture locus and the geometric center of all the recapture loci which are recorded for a particular grid of traps for a given individual. For brevity this distance is called the "recapture radius." The geometric center of the recapture loci is termed the "recapture center." These statistics are related to but differ somewhat from the respective center of activity and activity radius of the individual concerned. It should be pointed out that the various recapture radii for an individual are not independent of one another, since each recapture radius is a function of the recapture center. Accordingly,

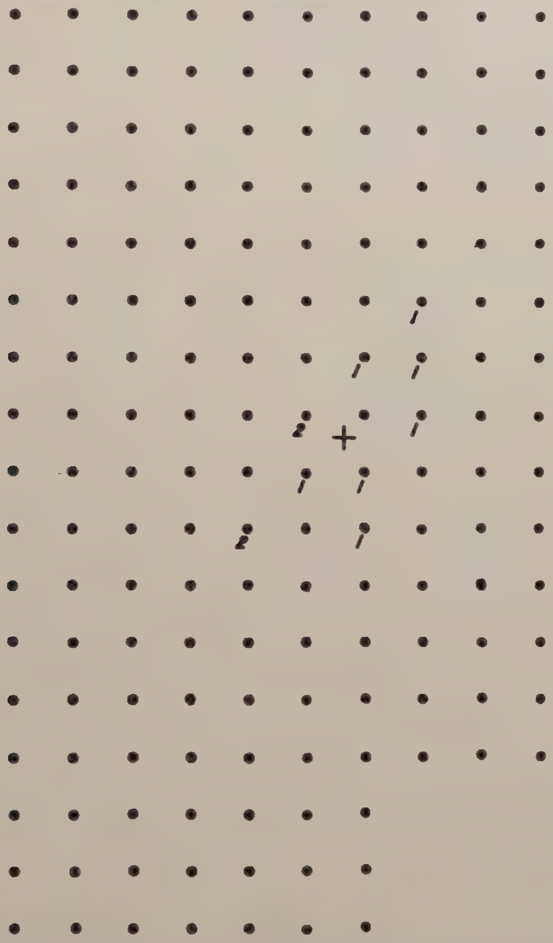


Fig. 1 Trap positions and recapture loci for adult female No. 1122, Peromyscus maniculatus bairdi, during October, 1951, on old-field study plot, E. S. George Reserve, Livingston County, Michigan. The cross marks the location of the recapture center. Distance between traps is 20 yards.

some small adjustment in the degrees of freedom for the variance of the recapture radii should probably be made (Fig. 1). Such an adjustment, however, has not been attempted in this paper.

Should an animal have been captured only once, its recapture radius is necessarily zero. Such a datum provides information concerning the activity center, but gives no information concerning the recapture radius of the individual. Consequently, in studying recapture radii it is useful to utilize only data including two or more captures of the same marked individual.

No upper limit can be assigned to a recapture radius, except that which is imposed by the dimensions of the trap grid; but the minimum value is always zero. Accordingly, if the grid is large enough to include completely the travels of an individual animal, it will not be surprising if the frequency distribution of the several recapture radii is positively skewed. Since the area of any circle of radius R is πR^2, the number of traps available in a circular area of radius $R^{1/2}$ is proportional to R, provided that the traps are equally spaced over the area; and this fact might also operate to produce a positively skewed distribution. Such considerations suggest that a square-root transformation might normalize the distribution of the recapture radii. At any rate, such a transformation might be expected to reduce the skewness sufficiently to enable the data to be used with the tabulated part of Pearson's type III probability distribution.

Let r be the recapture radius and let T be some transformation (such as the square-root transformation), which, when applied on r, produces a variable, X, distributed according to Pearson's type III probability function. Thus:

$$Tr = X \qquad (1)$$

and

$$T^{-1} X = r, \qquad (2)$$

where T^{-1} is the inverse of the transformation T. For Pearson's type III function:

$$c = \frac{\epsilon - \mu}{\sigma} \qquad (3)$$

whence

$$\epsilon = \sigma c + \mu, \qquad (4)$$

where μ and σ are the mean and standard deviation, respectively, of the population of X's, c is the standard variate of the Pearson type III distribution, and ϵ is any specified value.

If μ and σ were known, one could calculate, from equation (3) and a table of Pearson's type III distribution (with the proper skewness), the probability that a randomly chosen X would be less than ϵ. By using equation (4) together with the probability tables that value ϵ which is greater than a given proportion of the X's could be calculated. Having accomplished this, one could apply T^{-1} on X to obtain equivalent statements for r. In reality, however, neither μ nor σ can be known. These parameters can only be estimated. Consequently, from equation (3) one can only estimate the probability that a randomly chosen X will exceed a specified value ϵ, and from equation (4) one can only estimate that value ϵ which is exceeded by a given proportion of the X's. As the samples become larger the estimates improve, so that for samples of fair size, over 30, for example, the estimates of μ and σ may be fairly close to the actual parameters. For samples of such size, formulas (3) and (4) will provide acceptable and useful estimates of the probabilities and distances desired.

Although the preceding statements concern only the recapture radius of a particular individual, they may be generalized to treat the recapture radius of a population of individuals. For this purpose at least 2 recaptures per individual are required for a number of animals. When one individual is concerned, an attempt is made to ascertain the probability that a capture taken at random from the total number (>1) of captures available for that individual will be at a distance greater than r from the recapture center of the individual. On the population level we are concerned with the probability that a random capture of an individual taken at random from the total number of individuals available in the area will be at a distance greater than r from that individual's recapture center. Thus, if the area contains individuals $I_1, I_2, \ldots . I_i, \ldots . I_n$, and if for individual I_i the probability that a random capture will exceed a distance r from that individual's recapture center is p_i, then the probability that a random capture of a random individual will be greater than r from the individual's recapture center is:

$$P = \frac{p_1 + p_2 + \ldots + p_n}{n} .$$

It is the value of P which is sought for the population of animals. Unfortunately, the data available are usually too meager to permit accurate estimation of the p_i, and in such cases P cannot be ascertained by the rigorous method outlined above. We believe, however, that a reasonable approximation to P can be obtained by simply pooling all of the recapture radii obtained from the population and obtaining estimates of μ and σ from this pooled sample. We recognize that the validity of this procedure depends upon the assumption that the recapture radii for all of the animals form a single universe, which assumption we know to be not quite true. Nevertheless, this procedure has been followed in our study, in the belief that the error introduced by it is not appreciable.

APPLICATION TO TRAPPING RECORDS OF THE DEERMOUSE

To illustrate these ideas we have applied them to a set of trapping records of the prairie deermouse (Peromyscus maniculatus bairdi) from an old-field community on the Edwin S. George Reserve in southern Michigan. The trapping records have been kindly furnished to us by Francis C. Evans. A 10 x 17 matrix of traps, spaced 20 yards apart, was extended over this area. Each day the traps were checked

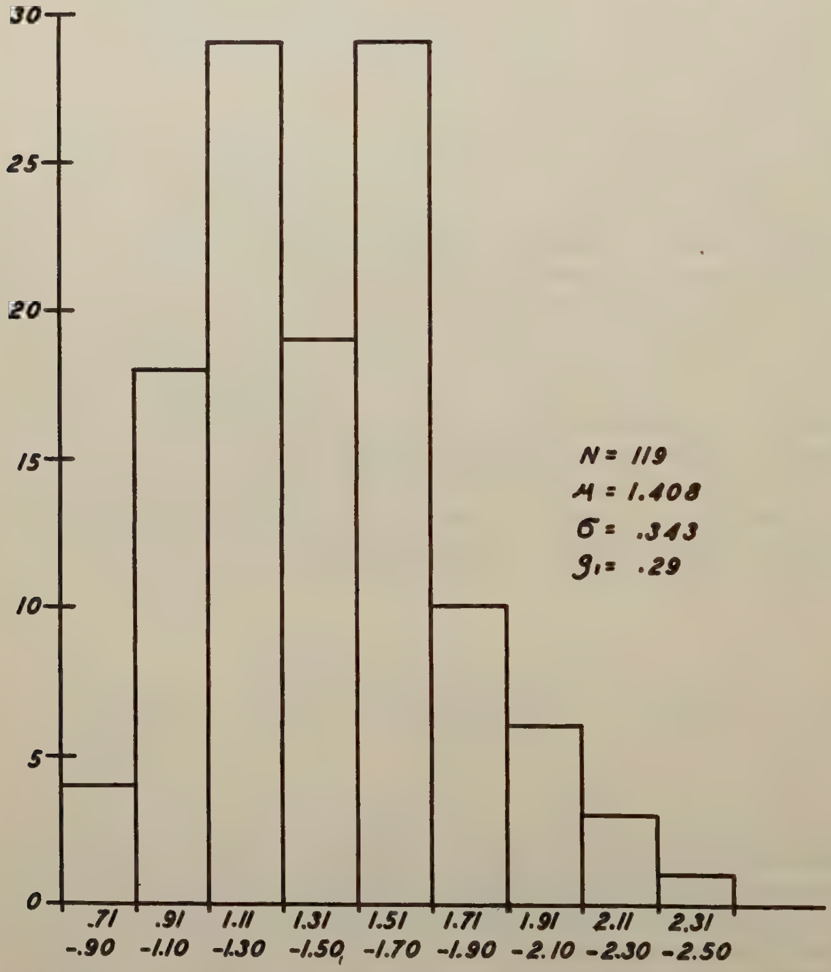


Fig. 2 Frequency histogram of square roots of recapture radii (1/2 distance between traps added to each recapture radius) in units of trap spacing (=20 yards); adults of Peromyscus maniculatus bairdi; during October of the four years 1948-51; on E. S. George Reserve, Livingston County, Michigan.

and each captured animal was marked, released, and its location recorded. This procedure was carried out for from 6 to 12 days in October of each of the four years 1948-51, inclusive (Fig. 2). Animals captured in peripheral traps were omitted from this study. During these periods 37 animals were captured two or more times, and a total of 185 recaptures was obtained. For each animal which was captured twice or oftener the geometric center of capture and the distance r of each capture from this center were calculated. In this manner 185 recapture radii were obtained. The square-root transformation was applied on r to produce a variable X (Table I). That is:

$$X = (r + 1/2)^{1/2} .$$

The 1/2 is added to each r before taking the square root as a correction for continuity (Kenney and Keeping, 1951, p. 253). Fisher's g statistics were applied to X in order to ascertain whether the distribution of the X's is nonnormal. The following results were obtained:

$$g_1 = .400 \qquad \sigma_{g_1} = .179 \qquad \frac{g_1}{\sigma_{g_1}} = 2.2$$

$$g_2 = -.093 \qquad \sigma_{g_2} = .356 \qquad \frac{g_2}{\sigma_{g_2}} = -0.3 .$$

It is seen that although g_1 differs significantly from 0 at the 5 per cent level, indicating positive skewness, g_2 does not so differ, indicating an absence of kurtosis. Consequently, an attempt may be made to fit X to the Pearson type III distribution. It is found that $\mu = 1.374$, $\sigma = .315$, and $\alpha_3 = .400$. Consequently, the deviation from the mean in units of σ is:

$$c = \frac{\epsilon - 1.374}{.315} .$$

This provides an estimate of the probability that a randomly chosen X will be less than any specified value ϵ, and the equation $\epsilon = .315c + 1.374$ will give an estimate of that value ϵ which is greater than a proportion P of the X's. For illustration the estimation of those values which are exceeded, respectively, by 25 per cent and 50 per cent of the X's will be described. From page 18 of Carver's tables (1940) it is found by interpolation for $\alpha_3 = .4$ and $P = .250000$ that c (called t in Carver's notation) $= -.706$. Thus, in this case $\epsilon = (.315)(-.706) + 1.374 = 1.15$. For $\alpha_3 = .4$ and $P = .500000$, it is found on page 20 that $c = -.067$, whence $\epsilon = (.315)(-.067) + 1.374 = 1.35$, and so

TABLE I

Transformed recapture radii for the prairie deermouse. Square-root transformation of distance of each recapture center of that individual, in units of space between traps.

Class and Individual Number	Recapture Order										
	1	2	3	4	5	6	7	8	9	10	11
1948 Adult ♀♀											
0004	.80	1.67	1.64	2.12	1.23	1.35					
0023	1.14	.92	1.14	.92							
Adult ♂♂											
0005	1.51	1.40	1.51	1.55	1.14	1.51	1.81	1.14			
0003	1.30	1.30	1.66	1.65	1.93	1.66	1.27	2.00	1.76		
0015	1.24	1.62	1.62	1.12	1.45	1.62	1.45	1.24			
Juvenile ♀♀											
0022	1.00	1.00									
0021	1.56	1.47	.91								
0002	1.85	1.10	1.59	1.10	1.10	1.46	1.13	1.59	1.76		
Juvenile ♂♂											
0024	1.10	1.10									
0020	1.18	1.18	1.48	1.02							
1949 Adult ♀♀											
0043	1.08	.91	.91								
0044	1.57	1.57	1.52	1.98	1.65						
0034	1.31	1.24	1.24	.89	1.24	1.46	1.58				
Adult ♂♂											
0041	1.60	1.23	1.96	1.86	1.68						
0040	1.26	1.29	1.26	1.29	1.03	1.72	2.13				
Juvenile ♀♀											
0042	1.26	1.29	1.59	1.61	1.59						
1950 Adult ♀♀											
0114	1.65	1.65	1.38	1.38							
1030	1.14	1.40	.92	1.14							
0123	1.96	1.71	1.63	2.18	1.33						
1000	1.31	1.15	1.48	1.57	1.15						

TABLE I (Cont.)

Class and Individual Number	Recapture Order										
	1	2	3	4	5	6	7	8	9	10	11
Adult ♂♂											
0113	1.66	.92	.92	1.83							
0041	1.06	1.45	.97	2.08	1.58						
Juvenile ♀♀											
1034	1.31	1.08	1.47								
1032	1.40	.92	1.14	1.14							
1025	1.16	1.39	1.16	1.11	1.72						
0042	1.68	.91	1.25	1.47	1.83	1.35					
0122	1.33	1.21	1.01	1.01	1.33	1.55					
1024	1.21	1.01	1.55	1.01	1.33	1.33					
Juvenile ♂♂											
1031	1.25	1.35	1.56								
1033	1.25	1.55	1.66	1.33							
1024	1.66	.92	1.14	1.55							
1951											
Adult ♀♀											
1132	1.00	1.00									
1131	1.00	1.00									
1135	1.47	1.83	1.35								
1120	.95	1.29	.95	1.90	2.41	1.29	1.55	1.05	1.76	1.45	
1122	1.68	1.11	1.80	1.56	1.11	1.38	1.38	1.68	1.19	1.11	1.48
Adult ♂♂											
1124	.71	.71									

forth. Thus, if P denotes any selected probability it is found that:

$$P\ (X < 1.15) = .25$$
$$P\ (X < 1.35) = .50$$
$$P\ (X < 1.57) = .75$$
$$P\ (X < 1.93) = .95$$
$$P\ (X < 2.20) = .99$$

Subtracting 1/2 from X^2 gives the following statements for the recapture radius (r):

$$P\ (r < .82) = .25$$
$$P\ (r < 1.32) = .50$$
$$P\ (r < 1.96) = .75$$
$$P\ (r < 3.22) = .95$$
$$P\ (r < 4.34) = .99$$

Similar estimates may be made for any other probability.

In the equations given above r is expressed in units of 1 trap space, that is, 60 feet, since the traps were spaced 60 feet apart in the grid. These equations allow the prediction that 25 per cent of the recaptures of the prairie deermouse from this grid will be less than 49 feet (i.e. .82 x 60) from the recapture center of the captured individual. Likewise, it can be predicted that 50 per cent of the recaptures will be less than 79 feet from the recapture center; 75 per cent of them will be less than 118 feet from this center; 95 per cent less than 193 feet; and 99 per cent will be less than 260 feet from it.

It can also be estimated that 25 per cent of the recaptures will be included in a circular area of 7605 square feet ($3.1416 \times .82^2 \times 60^2$) which is symmetric about the recapture center of the captured individual; 50 per cent of the recaptures will be included in a circular area of 19706 square feet symmetric about this center; 75 per cent within a circular area of 43448 square feet; 95 per cent within an area of 117,264 square feet; and 99 per cent within an area of 213,026 square feet. But these statements do not in any way imply that all parts of any circular area are equally occupied. It would certainly be desirable to know a great deal more about the movements of an animal than is provided in the statements given above. Nevertheless, these statements provide some useful information about the movements of the animals in question. Detailed statements will probably have to await more data.

It might be pointed out that the absence of platykurtosis in the pooled data suggests the validity of the assumption that these animals have no fixed home-range boundaries. Should there be a physical barrier to movement in one or more directions from the center of activity of an individual animal, this would be expected to result in limitation of the recapture radii in that direction or directions. Likewise, if the animals defend territories, their movements would be to that extent restricted and their recapture radii limited. In either case the result should be the occurrence of a certain amount of kurtosis in the frequency curve for the recapture radii. The absence of such kurtosis in our measurements indicates that home ranges of the prairie deermice on the trapping plot under consideration are not limited either by physical barriers or by territorial defense.

In order to ascertain how well the pooled data fit the Pearson type III distribution, a χ^2 test of goodness of fit was applied to them, using $\sigma = .315$, $\mu = 1.374$, $\alpha_3 = .40$, and appropriate values of c. Partitioning the data into 15 classes resulted in a χ^2 of 20.28, which, at the 5 per cent level, indicates significant heterogeneity. The existence of this heterogeneity suggests the desirability of investigating the effect of various factors upon the recapture radius.

RELATION OF CERTAIN FACTORS TO RECAPTURE RADIUS

Although the distribution of X is not normal at the 5 per cent level, it is considered that normality is approached sufficiently closely to enable a series of one-way analyses of variance to be applied to it.

The X's were first classified according to the years 1948, 1949, 1950, and 1951. A one-way analysis of variance reveals that the means of the X's for the various years do not differ significantly from one another at the 5 per cent level.

The 185 X's were next classified according to whether they pertained to ♂♂ or to ♀♀. The mean of the X's for the ♂♂ was 1.41 trapping units, and for the ♀♀, 1.35 trapping units; but the difference between the means of the 2 sexes is not significantly different from 0 at the 5 per cent level.

The X's were also classified according to age class, i.e., juvenile and adult. The mean of the X's for juveniles was 1.31 trapping units, for adults 1.41 trapping units; and the difference between these 2 means is significantly different from 0 at the 5 per cent level. Because the poor fit of the pooled data to the hypothetical distribution might be the result of combining juveniles with adults, these 2 age classes were now separately fitted. For juveniles $\sigma = .249$, $\mu = 1.312$, and $\alpha_3 = .26$. Partitioning them into 9 classes gave a χ^2 of 4.38, for which $.30 < P < .50$, indicating a satisfactory fit. For adults $\sigma = .343$, $\mu = 1.408$, and $\alpha_3 = .29$. Partitioning the adults into 11 classes resulted in a χ^2 of 7.57, for which, as with juveniles, $.30 < P < .50$, likewise indicating a satisfactory fit. It would appear desirable, therefore, to make estimates for juveniles and adults separately, whenever the data are sufficiently numerous to do so. Thus for juveniles:

$$P\left[\begin{matrix}X\\ r\end{matrix} < \begin{matrix}1.15\\ .82\end{matrix}\right] = .2658$$

$$P\left[\begin{matrix}X\\ r\end{matrix} < \begin{matrix}1.35\\ 1.32\end{matrix}\right] = .5763$$

$$P\left[\begin{matrix}X\\ r\end{matrix} < \begin{matrix}1.57\\ 1.96\end{matrix}\right] = .8507$$

$$P\left[\begin{matrix}X\\ r\end{matrix} < \begin{matrix}1.93\\ 3.22\end{matrix}\right] = .9892$$

$$P\left[\begin{matrix}X\\ r\end{matrix} < \begin{matrix}2.20\\ 4.34\end{matrix}\right] = .9992$$

and for adults:

$$P\left[\begin{matrix} X \\ r \end{matrix} < \begin{matrix} 1.15 \\ .82 \end{matrix}\right] = .2326$$

$$P\left[\begin{matrix} X \\ r \end{matrix} < \begin{matrix} 1.35 \\ 1.32 \end{matrix}\right] = .4511$$

$$P\left[\begin{matrix} X \\ r \end{matrix} < \begin{matrix} 1.57 \\ 1.96 \end{matrix}\right] = .6942$$

$$P\left[\begin{matrix} X \\ r \end{matrix} < \begin{matrix} 1.93 \\ 3.22 \end{matrix}\right] = .9290$$

$$P\left[\begin{matrix} X \\ r \end{matrix} < \begin{matrix} 2.20 \\ 4.34 \end{matrix}\right] = .9838$$

By taking the weighted mean of the juveniles and the adults for each of the above categories the following equations are obtained:

$$P\left[\begin{matrix} X \\ r \end{matrix} < \begin{matrix} 1.15 \\ .82 \end{matrix}\right] = .24$$

$$P\left[\begin{matrix} X \\ r \end{matrix} < \begin{matrix} 1.35 \\ 1.32 \end{matrix}\right] = .50$$

$$P\left[\begin{matrix} X \\ r \end{matrix} < \begin{matrix} 1.57 \\ 1.96 \end{matrix}\right] = .75$$

$$P\left[\begin{matrix} X \\ r \end{matrix} < \begin{matrix} 1.93 \\ 3.22 \end{matrix}\right] = .95$$

$$P\left[\begin{matrix} X \\ r \end{matrix} < \begin{matrix} 2.20 \\ 4.34 \end{matrix}\right] = .99,$$

which results agree closely with those obtained from the pooled data.

The X's were finally classified according to whether the individual to which they pertained was captured a total of 2, 3, ... , 11 times. An analysis of variance on this classification shows that the mean value of X for some of these categories differs significantly, at the 1 per cent level, from the mean value of X for other categories. Those animals captured fewer than 5 times had somewhat smaller recapture radii than those captured a greater number of times. It was suspected that this result might be caused by the fact that, in general, the more times an animal was caught, the greater the time interval between the first and last capture. If each individual's center of activity is absolutely fixed, and if the time interval between captures is sufficient to ensure that the positions of successive captures are essentially independent of one another, then the interval between the first and last capture should not bias the recapture radius. But if, as seems more likely, an individual's center of activity shifts somewhat with time, or if the interval between captures is so small that successive captures are not independent of one another, then one might expect the mean recapture radius to increase with the interval between captures. It was found that the interval between the first and last captures varied from 1 day to 15 days. An analysis of variance reveals a significant relationship, at the 5 per cent level, between the recapture radius and the interval between the first and last captures. Consequently, it would be most desirable if all of the data were uniform in this regard. If, however, only those records which were collected over a constant time interval were used, the data would be so greatly reduced that the final result would probably be less accurate than that obtained by pooling all of the recapture radii based on two or more captures.

It should be emphasized that any statements about recapture radii must apply only to a particular kind of animal in a particular location during a specified period, or periods, of time, and captured in a particular trap grid. The effect of variation in these factors upon the recapture radius can be learned only by experimentation. The effects of variation in year and likewise the effects of age class and of sex have been considered briefly. It would be interesting also to compare data from different localities. An especially interesting question is the effect of different trap spacings on the recapture radius. Hayne (1950) has found that the mean recapture radius of male meadow voles (Microtus) increases with the distance between traps, but such a relationship was not observed for the females. It seems certain that the distance between traps will influence the recapture radius, since if the traps are very far apart nearly all of the recapture radii will be zero; if the traps are quite close together they may hinder the movements of the animals to a great extent, thus perhaps reducing the recapture radius. But these matters require further experimental investigation.

Although our interest has been more in activity radii than in recapture radii, from the data available all of our knowledge of the former must be derived from the latter. It is likely that the mean activity radius is about 1/2 of a trap space greater than the corresponding mean recapture radius, since an animal probably wanders farther from its center of activity than the most distant trap in which it is caught, and it is probable that X^2 is a better estimate of the activity radius than is r. It should be re-emphasized, however, that nothing whatever can be learned from these data about the activity radii of animals which have not been influenced by the presence of traps.

SUMMARY

In the statistical concept of home range each animal is assumed to have a center of activity but no fixed outer limits to his range, except such as may be imposed by physical or biological barriers to his movements. In general, the greater the distance from his center of activity, the lower is the probability of the occurrence of that individual.

An "activity locus" is defined as one of an infinite number of points occupied by an animal in its movements over its home range. The "center of activity" is the geometric center of all of the activity loci. The distance between an activity locus and the center of activity for an individual is called an "activity radius." A "recapture locus" is defined as one of a finite number of points at which an animal is captured, and the "recapture center" is the geometric center of all of the recapture loci. The distance between a recapture locus and the recapture center is a "recapture radius."

These concepts are applied to the records of recapture of marked prairie deermice (Peromyscus maniculatus bairdi) on a grid of traps spaced at 60-foot intervals over a relatively uniform habitat on the Edwin S. George Reserve in southern Michigan. The square-root transformation, when applied to the several recapture radii, produces a variable, X, whose frequency distribution does not depart greatly from normality. Analysis of variance on the transformed variable, X, reveals no significant differences in mean recapture radii for the years 1948, 1949, 1950, and 1951. Males have a somewhat greater recapture radius than females, though the difference is not significant at the 5 per cent level. The recapture radius of adults is significantly greater at the 5 per cent level than that of juveniles. By use of Pearson's type III probability function it is estimated that of the recaptures of the prairie deermouse under the trapping conditions specified, 25 per cent will be within 49 feet of the recapture center, 50 per cent within 79 feet, 75 per cent within 118 feet, 95 per cent within 193 feet, and 99 per cent within 260 feet.

LITERATURE CITED

BLAIR, W. FRANK

1940 Home ranges and populations of the meadow vole in southern Michigan. Journ. Wildlife Management, 4:149-61.

BURT, WILLIAM H.

1940 Territorial behavior and populations of some small mammals in southern Michigan. Misc. Publ. Mus. Zool. Univ. Mich., 45:1-58.

CARVER, HARRY C.

1940 Statistical tables. Ann Arbor: Edwards Bros.

DICE, LEE R., and WALTER E. HOWARD

1951 Distance of dispersal by prairie deermice from birthplaces to breeding sites. Contrib. Lab. Vert. Biol. Univ. Mich., 50:1-15.

EVANS, FRANCIS C., and STANLEY A. CAIN

1952 Preliminary studies on the vegetation of an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 51:1-17.

HAUGEN, ARNOLD O.

1942 Home range of the cottontail rabbit. Ecology, 23:354-67.

HAYNE, DON W.

1949 Calculation of size of home range. Journ. Mammalogy, 30:1-18.

1950 Apparent size of home range of Microtus in relation to distance between traps. Ibid., 31:26-39.

KENNEY, J. F., and E. S. KEEPING

1951 Mathematics of statistics, Pt. II. New York: D. Van Nostrand Co.

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price $0.25.

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN

Number 63 April, 1953

ANTS OF AN OLD-FIELD COMMUNITY ON THE EDWIN S. GEORGE RESERVE, LIVINGSTON COUNTY, MICHIGAN

By MARY TALBOT

Accepted for publication December 2, 1952

CONTENTS

Introduction 1
Description of the Habitat 2
Methods of Study 3
General Distribution of the Ant Fauna 3
Abundance 5
Local Distribution Patterns 6
The Role of Ants in the Field Community 8
Summary 12
Literature Cited 13

INTRODUCTION

A STUDY of community dynamics has been initiated by the Institute of Human Biology, University of Michigan, with a long-term investigation of an old-field community on the Edwin S. George Reserve in southeastern Michigan. This program, begun in 1948, seeks to ascertain "the complete biota and the organization and operation of a natural community" (Evans and Cain, 1952). The present paper is a report of preliminary studies of the ants of that field made to find out what species are present and, as far as possible, what part they play in the life of the community. The work was done during the summer of 1951 and was assisted by a grant from the Edwin S. George Fund for Visiting Naturalists. Facilities of the Reserve were made available by J. Speed Rogers, Director, and Irving J. Cantrall, Curator of the Reserve. Francis C. Evans provided the necessary background knowledge of plants in the field and made many helpful suggestions for carrying out the work.

DESCRIPTION OF THE HABITAT

The field under study is a 15-acre tract in the central part of the Reserve and is bordered on the east and west by oak-hickory woods. Detailed studies of the vegetation (Evans and Cain, 1952; Cain and Evans, 1952) show that the field is essentially a Poa compressa-Aristida purpurascens grassland community. These grasses are mixed with a variety of other plants which are distributed unevenly in such a way as to give the field a mosaic appearance. In some places the panic grasses form circles of light green, in others dry heads of Lespedeza rise several feet, and in still others flowers of Asclepias, Liatris, Monarda, Solidago, or Potentilla are conspicuous in their season.

The topography consists of ridges and miniature plateaus alternating with shallow depressions which in some places are as much as 5.5 feet deep. These low swales collect enough organic matter and hold enough moisture to maintain a thick growth of Kentucky bluegrass (Poa pratensis). Over most of the field, however, sterile soil and rapid drainage allow only the relatively sparse growth of the upland vegetation.

The field has a barren aspect in certain places where grasses are almost completely replaced by plants which grow close to the ground. These consist chiefly of large clones of mosses (mainly Polytrichum and Ceratodon), lichens (primarily species of Cladonia), or the composite Antennaria. The aspect of barrenness is increased by scattered patches of soil, many of which are the result of rodent and ant digging.

Major succession of the field back to oak-hickory forest seems to be slow. Evans and Cain (1952) have pointed out that this is probably due to the sterility of the soil and the effects of overbrowsing by a herd of deer. Small hickories, oaks, and cherries, and scattered junipers and hawthorns suggest, however, that in time the field will revert to a deciduous forest.

Short-term vegetational changes within the field itself, called "micro-successional cycles" by Evans and Cain (1952), are of more immediate interest because of the part ants play in their development. The progress of one of these cycles is essentially as follows: colonies of such mosses as Ceratodon and Polytrichum, or of the close-growing Antennaria, or of certain grasses invade any patch of bare soil and form a pioneer stand of low, dense-growing vegetation. Soon these patches are taken over by Poa compressa and scattered representatives of other grasses and forbs. After these have flourished for a time, the accumulation of dead culms retards further growth of grass and produces conditions favorable for lichens such as Cladonia. The lichens do not seem to prevent erosion by rain, wind, frost, or animal activity and they are frequently covered in a short time by fresh soil, thus preparing the way for a repetition of the cycle. Ant digging was found to be responsible in many cases for the small areas of bare soil on which these cycles are initiated.

METHODS OF STUDY

In a field entrances to ant nests are often thoroughly concealed. In order to find colonies, cake crumbs were scattered, and ants were followed as they carried them to the nests. Each nest so found was marked with a stake and recorded on squared paper. This technique was quite accurate for Myrmica, Aphaenogaster, and Formica, but not so successful for Lasius, Solenopsis, and Monomorium. The last two are small and often did not forage aboveground; their colonies were hunted by removing small stones or by bending plants to one side. It is probable that the number of Solenopsis and of Monomorium colonies recorded represents an undercount. In contrast, Lasius figures doubtless represent an overcount because of the difficulty in distinguishing limits of colonies. For this study each crater of soil which had ants going in and out of its entrances was recorded as a separate colony. Although it is known that a single colony may have more than one such active crater, no one has determined how extensive a Lasius colony is (Headley, 1941).

The abundance and distribution of ant colonies were determined by two principal methods. The first concerned the location of colonies in each of 25 staked plots selected to include as many types of plant associations as possible. The area of each plot was 10 square meters. This method provided information about the comparative densities of the various ant species in the several plots. The second method consisted of locating colonies throughout somewhat larger areas selected for their particular topographic positions. To determine the influence of swales or shallow depressions in the field upon ant distribution, colonies were staked along a transect through a swale and up its slopes to nearby ridges. Another group of colonies was studied at the west edge of the field, in order to evaluate the influence of a bordering woods. This second method yielded information about the factors affecting local distribution patterns.

GENERAL DISTRIBUTION OF THE ANT FAUNA

The 16 species of ants listed in Table I were found nesting in the field. Detailed studies centered around the first seven because they were common and typical species of field ants which affected the field relationships to the greatest extent. Of these, Lasius niger neoniger[1] was perhaps the most widespread. It did not maintain colonies in the thickly grassed swales and was less abundant in shaded areas but was the most conspicuous ant in every other part of the field. It seemed especially well adapted to the driest, most barren parts. Myrmica

[1] These are the Lasius with erect or suberect hairs on their antennal scapes which run to neoniger in Creighton's (1950) keys. They have been examined by E. O. Wilson who is revising the forms of Lasius (Lasius) and who states that they are americanus Em.

americana, Solenopsis molesta, and Monomorium minimum were almost as widely distributed but they were not so well adapted to the driest areas and thus flourished in the moister places, being found even in the bottom of swales. Aphaenogaster treatae, Formica neogagates, and F. pallidefulva nitidiventris (= F. p. schaufussi incerta before Creighton, 1950), also typical field ants, were widespread on the slopes and ridges covered with sparse stands of Poa compressa which spread over most of the field but did not thrive in the driest or in the most moist places.

The other nine species found in the field seemed to be of minor importance. Prenolepis imparis was found several times in June but then disappeared to stay below ground and was not seen again until apples began to ripen near the field late in August. This is a cold-weather ant, and it may play a more active part in the field ecosystem in early spring and late autumn. Formica lasioides was found several times but certainly was not numerous. Six colonies of the blood-red slave maker, Formica rubicunda, were known to exist on the field, and these

TABLE I

Ants of an Old-field Community on the Edwin S. George Reserve, from a Study Made in the Summer of 1951

Typical field ants — widespread and numerous:

1. Lasius niger neoniger Emery
2. Myrmica americana Weber
3. Aphaenogaster (Attomyrma) treatae Forel
4. Formica (Proformica) neogagates Emery
5. Formica (Neoformica) pallidefulva nitidiventris Emery
6. Solenopsis (Diplorhoptrum) molesta (Say)
7. Monomorium minimum (Say)

Field or border ants — not numerous:

8. Prenolepis imparis (Say)
9. Formica (Proformica) lasioides Emery
10. Formica (Raptiformica) rubicunda Emery
11. Polyergus lucidus Mayr

Ants invading the field border — of local distribution and limited abundance:

12. Formica fusca Linne
13. Camponotus pennsylvanicus (DeGeer)
14. Aphaenogaster (Attomyrma) rudis Emery
15. Myrmica emeryana Emery
16. Ponera coarctata pennsylvanica Buckley

made conspicuous raids on F. neogagates. The one colony of the shining slave maker, Polyergus lucidus, enslaved F. p. nitidiventris.

Ants of the field border seemed to require shade for at least part of the day and prospered under a leaf covering. Consequently, the three large hickory trees left by the settlers who cleared the field formed islands for these forms. The following border ants can be expected to increase in number as the field reverts to woods: Myrmica emeryana will replace M. americana, Aphaenogaster rudis will increase as A. treatae dies out, and Formica fusca will take the place of F. neogagates and F. p. nitidiventris. Camponotus pennsylvanicus will nest wherever logs are present, and Ponera coarctata pennsylvanica will live in decaying wood or under leaves in soil.

ABUNDANCE

The results of the examination of 25 selected 10-square-meter plots are shown in Table II. The most widely distributed species were also the most abundant in numbers of colonies found. Lasius niger neoniger is undoubtedly the most abundant species on the field although the 125 active craters recorded for it probably represent an overcount of colonies; its circles of bare soil certainly made it the most conspicuous. Myrmica americana, with 58 distinct colonies, was second in abundance. Aboveground, Myrmica workers were more numerous and widespread than those of Lasius; the former foraged continuously as long as temperature permitted, but the surface activity of the latter was largely confined to bringing up more soil.

The importance of Aphaenogaster treatae in the field seemed greater than the figures indicate. Individuals of this species foraged for fairly long distances (9 to 12 feet) from the nest, gathering a great variety of food, and colonies were never close together. Formica neogagates and F. p. nitidiventris displayed patterns of distribution and habits much like those of Aphaenogaster. F. p. nitidiventris workers were very conspicuous foragers, especially in hot weather when all other species were below ground. This habit of long-distance foraging enabled a single colony to patrol a large surface area, and it is not surprising that colonies of these species were not clustered together.

When the entire ant fauna is considered, there is a mean of approximately one colony per square yard for the 299 square yards (250 square meters) studied in the 25 plots. Average areas for single colonies of each species ranged from 2 square yards for L. n. neoniger and 5 square yards for M. americana to 23 square yards for F. neogagates, 50 square yards for A. treatae, and 60 square yards for F. p. nitidiventris.

Calculations of actual numbers of ants in the field presented greater difficulties, for there was much variation in the size of colony populations, not only among species but also among the colonies of any one species. The most practical attack on the problem of total population would seem to be to determine average populations for each species.

No direct determination of numbers was attempted on the field, and no colonies were dug since it was desired to avoid any disturbance of the soil. The only population figures available are for F. p. nitidiventris and A. treatae. Individuals of F. p. nitidiventris were not counted at the Reserve, but 24 colonies dug at the University of Michigan Biological Station (Talbot, 1948) were probably similar in size. They were found to average 2352 individuals (eggs, larvae, pupae, adults), of which 855 were workers. If, at the Reserve, there is a general distribution of one colony for each 60 square yards, then the field should support a population of approximately 1320 colonies of this species and consequently 3,000,000 individuals of which over 1,000,000 are workers. Several A. treatae colonies were dug at the Reserve during the summer of 1952 in an area directly adjoining the study field. Colonies averaged 1331 individuals, 682 of which were workers. If there is a general distribution of one colony for each 50 square yards, there are, in the field, 1584 colonies comprised of approximately 2,100,000 individuals, of which 1,000,000 are workers.

LOCAL DISTRIBUTION PATTERNS

To determine whether or not there were differences in vertical distribution shown by the various species, ant colonies were staked through a moist swale and up its slopes to the drier ridges above. The selected swale consisted of an oval area supporting a thick stand of Kentucky bluegrass about 16 yards long and 9 yards wide from which the ground rose on all sides to form ridges 4.4 to 5.4 feet high and 20 to 30 yards away from the swale. On the slopes Poa compressa was the dominant plant, interspersed with a variety of other grasses, forbs, mosses, and lichens, all distributed sparsely enough to allow the bare sandy loam to be seen.

For this study four species were considered (M. americana, F. neogagates, F. pallidefulva nitidiventris, and A. treatae), and their nests were staked on the east, west, and north slopes. In all, 125 colonies were found in an area of about 800 square yards. M. americana was most abundant with 78 colonies, or one colony every 10 square yards; F. neogagates had 20 colonies, or one colony for each 40 square yards; A. treatae was more sparsely distributed with 14 colonies, or one for each 57 square yards; and F. p. nitidiventris had 13 colonies, one for each 61 square yards. This agrees with the plot survey in relative abundance of colonies of the four species, but shows a less dense distribution.

There was some evidence of differential vertical distribution, as indicated in Table III. Myrmica colonies were most abundant on the lower parts of the slopes, whereas the other three species flourished higher up. The dense matted grass of the swale bottom proved unfavorable for ant nests; a survey of 10 square meters in its center revealed only four M. americana colonies and two of Solenopsis molesta. Myrmica colonies were most abundant in a ring just above the bottom of the swale; evidently soil and vegetation conditions in the sparser grass were better for their nests. The two F. neogagates colonies listed for the lowest level were also not in the swale itself but were about a foot above it. No Lasius craters were found at this level or in the swale, but they were numerous in all parts at higher levels.

The abundance and variety of food available within the swale may have influenced nest locations. Ants were seen to carry spiders, crickets, beetles, leaf hoppers, larvae of various kinds, and parts of grasshoppers. Aphids were numerous on the leaves of milkweed (Asclepias syriaca). M. americana was particularly conspicuous as a forager here; it was joined by F. p. nitidiventris, which came down the slopes from longer distances, some as much as 18 yards. In addition to a plentiful food supply, temperature conditions in the swale were ideal for foraging because the thick stand of grass retained the night's coolness and cut off the sun's rays. At 11:30 A.M. on July 19, for example, temperature in the sun on the ridge was 98° F., when in the swale it was only 78° F.

TABLE III

Differential Vertical Distribution of Ant Colonies from a Swale to a Ridge - a Rise of 5 Feet 5 Inches, E. S. George Reserve, Summer of 1951

Species	Height of Level Above Bottom of Swale		
	0'-1'5"	1'5"-3'5"	3'5"-5'5"
Myrmica americana . . .	40	24	14
Formica neogagates . . .	2	8	10
Aphaenogaster treatae . .	0	6	8
Formica pallidefulva nitidiventris	0	6	7

Studies of the field border nearest the woods showed that woodland ants were invading the field concomitantly with woodland plants. Camponotus pennsylvanicus, which requires wood for its nests, was found foraging on the field's edge, and one small colony was discovered nesting in a branch under a hickory tree in the center of the field. A Formica fusca mound was found under the same tree, and several others occurred just off the field at the wood's edge.

Aphaenogaster rudis and Ponera coarctata pennsylvanica, abundant in the woods, were able to maintain themselves at the field's west border where there was a rather permanent ground covering of oak leaves. Myrmica emeryana seemed the most successful of the border ants; a group of colonies was found at the northwest corner of the field and another group on the west side of a hickory tree, both in the shade of overhanging branches and in an area of thick grass, mixed with a layer of dead grass stems, tree leaves, and twigs.

The west border of the field proved best for ant invasion because it afforded three conditions not common to the field proper: (1) a scattering of little oak trees, (2) a sparse but distinct covering of oak leaves blown in by a prevailing northwest wind, and (3) afternoon shade from the nearby woods supplemented by little areas of moving shade from the small trees. The hickory trees in the field's center duplicated conditions of shade and ground cover.

THE ROLE OF ANTS IN THE FIELD COMMUNITY

Nest building and its effects. — Soil was the only habitat available for ant nests. Not only were there no sizable logs, but the extreme fluctuations of surface temperature prevented ants from nesting in matted or upright stems. Thus, the typical field ants were all soil-dwelling forms.

Lasius niger neoniger nest entrances were by far the most easily located, for although workers spent most of their time underground, they were constantly bringing soil to the surface, so that each nest entrance was surrounded by a crater of bare soil. Their nest-building activity seemed to play an important part in microsuccession. As pellets of soil were piled up to form craters around nest entrances, lichens and mosses were buried and often killed. Lasius seems, therefore, to shorten the declining or lichen stage and to retard the development of the pioneer stage, thus prolonging the bare soil period of microsuccession. The piles of bare soil also contribute to the process of leveling the field. During rains the soil was washed down, and as it dried it was blown by the wind. Soil was deposited in depressions, which were thereby raised at the same time that the ridges were being lowered.

The soil of 20 Lasius craters observed in the plot survey was collected to learn how much was brought to the surface. The average crater was 13 cm. long and 11 cm. wide, with a center 2 cm. high. The average volume of soil per crater was 164 cubic cm., and the average weight was 171 grams. These data, together with a mean crater density of 5.00 per 10-square-meter plot, show an estimated average soil displacement of 82 cubic cm. or 85.5 grams per square meter of surface area. If these figures are applicable to the entire field, Lasius is responsible for the displacement on each acre of approximately 12 cubic feet of soil weighing 750 pounds.

The ants were continually abandoning entrances and making new ones; they excavated soil all through the summer except in extremely dry weather. To illustrate this, one plot was studied four times during the summer. On June 23, after a rain and at moderate temperature which allowed full surface activity, there were 17 active craters and 8 inactive ones. A week later, after another hard rain, there were again 17 active craters but only 12 of them were those staked the week before. Later (August 8), after a dry period, 5 old craters were still in use, 7 had been abandoned, and there were 5 new ones, making a total of 10 active craters. The dryness continued, and a week later only 6 active craters were found, although the count had been taken early in the morning at favorable temperature (66° F.). Thus, the number of craters in this plot varied from 6 to 17, depending on the amount of excavating the ants were doing. Excavating activity, in turn, was conditioned by moisture and temperature. Any rain after a dry period caused new craters to be thrown up.

In contrast to entrances of Lasius nests, those of Aphaenogaster treatae were quite inconspicuous. This ant was most abundant in areas of sparsely growing grasses, such as Poa compressa, Aristida purpurascens, and Panicum depauperatum, and could not tolerate heavy swale stands of Poa pratensis. Nest entrances were large, often 1 to 1.5 cm. across, but they were usually so thoroughly concealed by blades of dead grass or overhanging lichen that they were found only when the ants entered carrying crumbs. Entrances usually slanted under roots of grasses; sometimes there were two, one on each side of a grass clump. Frequently, before the entrance there was a little depressed runway of more or less cleared soil beyond which might be a heap of excavated soil pellets or perhaps the discarded seeds of Panicum depauperatum or of mullein flowers if the workers happened to be collecting these. The entrances usually led to a large superficial chamber, sometimes entirely aboveground and roofed by upright or matted grass blades plastered together by soil pellets, sometimes sunk into the soil for as much as 5 cm., but still covered by the light, compact thatch roof or by a crust of lichen or moss. These chambers were usually not distinguishable from the common litter of dead grass stems lying on the ground. Chambers varied in floor area from 3 by 5 cm. to 3 by 15 cm., and from 2 to 5 cm. in height, and were usually irregular in shape. They were interlaced by grass stems and roots from around which the soil had been removed. From the superficial chamber 2, 3, or 4 large galleries led down to another large chamber from which descended one or more galleries. The impression was always that of large spaces around the grass roots, a condition which tended to increase the rapidity of drainage and thus to prevent the growth of thick stands of grass, and which during dry weather must have hastened the death of the vegetation. The effect of Aphaenogaster nests on the development of microsuccessional changes seems, therefore, to be one of terminating the grass stage and of including the degenerative lichen stage.

Myrmica americana nests seemed quite similar to those of A. treatae with respect to their influence on microsuccession. Surface chambers again made large spaces around the roots and resulted in increased drainage and drying. Myrmica entrances were unique in that most of the colonies built chimneys 0.5 to 1 cm. high, of woven grass blades or bits of lichen stuck together with soil pellets.

Formica neogagates nest entrances were even more inconspicuous and were never found until ants were seen entering them. They consisted of openings of 0.5 cm. or less, concealed under bits of lichen or grass. Small galleries sloped directly into the soil with no surface chambers. In contrast, compound colonies of F. neogagates and F. rubicunda were conspicuous. One small colony had thrown up a circle of soil 13 by 15 cm. and 0.5 to 2 cm. high, bare except for six stalks of

P. compressa and one of Rumex Acetosella. A larger colony had formed a bare area 35 by 30 cm. pierced only by several P. compressa and stunted, withered Rumex. The crater of this colony had four openings at its center, which was 3 cm. high, and three other openings about its rim. The bare soil seemed much hollowed out by chambers just below the surface, and Rumex roots growing through them were covered with root aphids. These nests also seemed to have the effect of eliminating the microsuccessional grass stage.

A nest of Formica pallidefulva nitidiventris usually had one entrance, often partly concealed by vegetation, with a small mound of excavated soil near by, sometimes as far as 15 cm. away. Previous study at the University of Michigan Biological Station showed that nests of this species may have from 2 to 5 galleries extending as deep as 30 to 40 inches.

Food and foraging habits. — The ants were primarily scavengers and patrolled the ground so thoroughly that dead animals were never allowed to litter it. Insects were the most abundant source of food and formed the main part of the diet, but spiders were also frequently collected, and one dead ground squirrel was found covered with Solenopsis molesta. Sometimes injured or slow-moving insects were collected alive.

Secretions of root and stem aphids formed a second important source of food. Lasius niger neoniger depended on root aphids for their main food and were found foraging at the surface only during cool, damp weather; Myrmica americana and Formica neogagates were seen frequently on stem aphids of milkweeds. Flower nectar formed a third source of food, and milkweed flowers were especially attractive to M. americana, F. neogagates, F. p. nitidiventris, F. lasioides, L. n. neoniger, and Prenolepis imparis. F. p. nitidiventris also seemed to collect milkweed juice from breaks in the stem.

At the time when mullein (Verbascum thapsus) was in bloom, A. treatae collected petals by pulling them from the flowers. These were found fresh and intact on the refuse piles, and it is not known whether any were used for food. During the first half of July, when seeds of Panicum depauperatum were ripening, certain colonies of M. americana and A. treatae appeared to make harvesting of the seeds their main activity. Members of one colony were observed to be bringing in one or two seeds a minute. Curiously enough, other workers of the colony were carrying seeds out of the nest at about the same rate and depositing them on discard heaps a few inches away. Under the microscope these seeds seemed to be just as whole and good as those being brought in by foraging ants. Many colonies in the P. depauperatum areas accumulated little mounds of seeds outside the nests. Later, after rains, some of the seeds sprouted, so perhaps in this instance the ants were favoring growth of the panic grass. Seed harvesting and flower attending were seasonal, but the collecting of dead insects went on day after day during the entire summer.

The foraging activities of the various species of field ants resulted in a 24-hour patrol of the ground surface. L. n. neoniger workers did most of their surface foraging during the night. In the early morning and late afternoon the field was predominantly populated by M. americana and A. treatae, but at midday F. p. nitidiventris and F. neogagates were often the only ants seen. This division of time for labor was dependent on reaction of the species to fluctuations in temperature, which were especially marked on the open field, there being little to form a shield against the direct rays of the sun. L. n. neoniger workers did not forage much aboveground except when temperature was low and humidity high. Consequently, they could forage during many nights but were kept below ground during all but cool, cloudy days. M. americana and A. treatae foraged at medium temperatures, but F. p. nitidiventris and F. neogagates did not reach full foraging force until temperatures were high.

Surface temperature readings were taken to determine the critical temperatures for some species. The following examples seem typical. M. americana were being watched one afternoon when moving clouds made alternate sun and shade, and temperatures fluctuated above and below the ants' critical range. At 84° F. Myrmica workers foraged actively and at 88° F. they could still walk across the sunny patches to the nest, but at 92° F. they were unable to traverse the hot soil and kept circling in the shade or climbing grass blades. At 94° F. no ants were in sight. Approximately 90° F. seemed, therefore, to be the limiting temperature. Ants trapped out of the nest during the heat of the day clustered just below the soil surface among the roots of grasses or forbs. A. treatae reacted in a similar manner but could tolerate slightly higher temperatures.

F. p. nitidiventris and F. neogagates did little foraging until the ground temperature reached 80 F. Observation on an afternoon when sun temperature on the ground was 96 F. and shade temperature was 82 F. showed that F. neogagates workers were proceeding normally to and from their nests, whereas M. americana individuals were immobilized, apparently trapped by the heat of any spot of bare sunny soil. One hour later, when surface temperatures had risen to 106° F. in the sun and 86° F. in the shade, even the F. neogagates workers were unable to reach home.

These variations in reaction to temperature illustrate differences in adaptation to field life and offer a partial explanation for the coexistence of so many different species. L. n. neoniger has become essentially independent of the ground surface through its cultivation of root aphids and is rarely exposed to extreme heat. M. americana and A. treatae are ground surface foragers but confine their activity to periods of moderate temperatures; such periods are long enough and occur frequently enough for these species to maintain themselves. F. p. nitidiventris and F. neogagates are adapted to withstanding higher temperatures, and their foraging time was cut by even a moderate drop in temperature.

Parasitism and predation. — Parasitic orange mites infected all four species of Formica. Spiders captured some ants, and a tiger beetle (Cicindela sp.) was watched as it pounced upon an ant and ate it. Flickers (Colaptes auratus) were found opening Myrmica nests in other parts of the Reserve but were not observed on this field.

SUMMARY

A survey of the ant fauna of an old-field community on the Edwin S. George Reserve revealed the presence of 16 species. Seven of these were common and typical field forms, four were less numerous and were found sparingly in both open-field and field-border situations, and five were present only in the proximity of adjacent woods or under the shade of large isolated hickory trees. The border species appear to be gradually replacing the typical field forms as the field reverts to oak-hickory woodland.

Examination of 25 selected 10-square-meter plots indicated that Lasius niger neoniger was the most widespread and numerous species, with an average density of five colonies (active craters) per plot. Comparable densities for the other typical field ants were as follows: Myrmica americana, 2.32; Solenopsis molesta, 1.80; Monomorium minimum, 0.60; Formica neogagates, 0.52; Aphaenogaster treatae, 0.24; Formica pallidefulva nitidiventris, 0.20.

The distribution patterns of several species were studied by local surveys. The dense growth of Poa pratensis in shallow depressions or swales was unfavorable for ant nests. Myrmica colonies were most abundant on the lower parts of the slopes of these swales, whereas Aphaenogaster and Formica flourished higher up. The west border of the field provided the most favorable conditions of shade and cover for the invasion of woodland ants.

The craters of soil brought to the surface during the construction of Lasius nests were estimated to represent an average displacement of 82 cubic centimeters or 85.5 grams per square meter of surface area. One of the principal effects of this activity was apparently to encourage and prolong the development of the more barren stages of microsuccession. Subsurface chambers formed by the nest building of Aphaenogaster, Myrmica, and Formica produced large drainage spaces around the roots of grasses and forbs and tended to prevent the growth of dense stands of vegetation.

Foraging by ants kept the field clear of dead animals. Insects and the secretions of root and stem aphids were the principal foods. Plant materials collected included seeds, nectar, and parts of flowers.

Variations in temperature seemed to control the foraging hours of the different ant species. Lasius foraged only during cool, damp weather; Myrmica and Aphaenogaster confined their hunting to periods of moderate temperatures; the typical field Formicas are evidently adapted to withstanding higher temperatures. The differences in reaction exhibited by the various species resulted in a constant patrol of the field.

Mites were found on all four species of Formica. Ant predators included spiders, tiger beetles, and the flicker.

LITERATURE CITED

CAIN, STANLEY A., and FRANCIS C. EVANS

1952 The distribution patterns of three plant species in an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 52: 1-11.

CREIGHTON, WILLIAM STEEL

1950 The ants of North America. Bull. Mus. Comp. Zool., Harvard College, 104.

EVANS, FRANCIS C., and STANLEY A. CAIN

1952 Preliminary studies of the vegetation of an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 51:1-17.

HEADLEY, A. E.

1941 The study of nest and nesting habits of the ant Lasius niger subsp. alienus var. americanus Emery. Ann. Entomol. Soc. Amer., 34(3): 649-57.

TALBOT, MARY

1948 A comparison of two ants of the genus Formica. Ecology, 29(3): 316-25.

Lindenwood College, St. Charles, Missouri

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price, $0.25.

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

UNIVERSITY OF MICHIGAN, ANN ARBOR, MICHIGAN

Number 64 February, 1954

THE SOIL ARTHROPODS OF A FIELD IN SOUTHERN MICHIGAN: A STUDY IN COMMUNITY ECOLOGY

By NELSON G. HAIRSTON and GEORGE W. BYERS

Accepted for publication April 7, 1953

CONTENTS

Introduction 1
Description of the Field 3
Methods 3
Numerical Abundance of Microarthropods 4
Vertical Distribution of Microarthropods in the Soil 6
Distribution on the Field 8
Seasonal Variations in Numbers and Vertical Distribution 16
Relationship Between Numbers of Individuals and of Species 25
Summary and Conclusions 34
Literature Cited 35

INTRODUCTION

PROBLEMS of analyzing a natural community are so great and so numerous that one would seem foolhardy to attempt their solution. Nevertheless, the attempt is made worth while by the fact that the natural community represents the major framework for a great deal of ecological thought. We use grandiose terms and abstract ideas in speaking of major communities, biocoenoses, associations, and so forth, and then quietly go back to our work on the ecology of a few taxonomically limited species. Plant ecologists and limnologists have made the major contributions to current ideas concerning communities. The reason is not far to seek. The student of the animals of terrestrial communities has no Gray's Manual nor Ward and Whipple to orient him taxonomically. As a consequence, such an ecologist follows one of three approaches: (1) He selects a small taxonomic group, becomes proficient in naming the members of that group, and works out their ecology in such detail as he can; (2) he lumps everything together that he does not recognize; (3) he sends his material to competent taxonomists for identification. The third approach would seem to be the best course, except for a few obstacles. The taxonomists are imposed upon; there are many groups not covered by competent taxonomists; and the amount of time involved is enormous. As the result, when the ecologist begins to write up his work he finds that for some groups he has specific or even subspecific identifications, but for other groups the identifications may be only to genus or other higher categories. Unfortunately, ecological importance and taxonomic certification may thus eventually have an inverse relationship.

In the present work we have attempted to cut the Gordian knot of taxonomy by sorting out the kinds of small arthropods that were recovered by Tullgren extractions, making no effort to identify them beyond higher categories. Below this level they are referred to by letter and number. The letter indicates the presumed next lower category; the number refers to the order in which the kind appeared in the process of counting. Thus, mite P1 is the first kind of Parasitoid found; Beetle St3, the third kind of Staphylinid, and so forth. The kinds were sorted with extreme care, and mounted specimens were used in checking identities. We are confident that the kinds recognized were kept consistent. In order to provide a basis for reference, specimens of each kind will be deposited in the Museum of Zoology of the University of Michigan. This procedure, although admittedly less desirable than perfect taxonomic identification, we believe to be superior to methods involving the lumping of numbers of species. The real question, of course, is whether the kinds that we recognize are the equivalents of the true species present. We believe that the great majority of them are. It may be argued that confusion will occur between the young and adults of the same species, but over 95 per cent of the individuals counted were either mites or ametabolous insects; the young in these cases are usually similar to the adults. Life-history stages have presented no problem serious enough to bias the results. It may also be argued that one unfamiliar with specific characters would not know what to look for in sorting the kinds. This is undoubtedly true in general, but many competent taxonomists are agreed that for a restricted locality the problem of sorting is greatly reduced. Granting some errors, particularly with metabolous insects and sexually dimorphic species, we believe that they are few and unimportant to the study as a whole. Throughout the remainder of this paper we shall assume that the organisms are sorted correctly to species, and we shall refer to them accordingly.

Acknowledgments

This study was supported by a grant from the Horace H. Rackham School of Graduate Studies: Faculty Research Fund, Project No. 739. We are indebted to J. Speed Rogers, Director of the Edwin S. George Reserve, for making the facilities of the Reserve available. Irving J. Cantrall, Curator of the Reserve, assisted in many aspects of the field work. Frederick E. Smith kindly spent many hours with the senior author, discussing the statistical analyses.

DESCRIPTION OF THE FIELD

The abandoned field upon which these observations were carried out is situated on the Edwin S. George Reserve in the southernmost part of Livingston County, Michigan. The Reserve has belonged to the University of Michigan since 1930 and has not been disturbed since that date. The field was probably used as pasture prior to its acquisition by the University and has apparently not been ploughed for at least 50 years (Evans and Cain, 1952). Rectangular, and oriented approximately north and south, it contains 14.5 - 15 acres (Fig. 3). The vegetation is principally grass, with a scattering of juniper and hawthorn shrubs. The surface is flat, broken in 11 places by shallow depressions, the vegetation of which is markedly different, being a dense mat of bluegrass (Poa pratensis), with few other herbs. Detailed studies of the vegetation have been undertaken, and some of the results have been published (Evans and Cain, 1952; Evans, 1952; Cain and Evans, 1952).

The field is on upland glacial outwash; the soil has been classified as sandy loam of the Fox or Bellefontaine series. The major part of the sod ends at about 1.5 inches; below this, there is a zone of the same dark brown, but of coarser texture, extending to 7.5 - 8 inches. This band ends abruptly, giving way to an orange sand containing waterworn stones up to 3 inches in diameter, most of them about 1 inch. The orange sand gradually becomes darker and extends down to 32-40 inches. It gives way to a sandy gravel which is light gray to tan. This is again an abrupt change. The gravel goes to at least 48 inches; it is the only layer that gives a positive reaction for carbonate. The soil profile in the depressions differs principally in the greatly increased thickness of the different layers.

METHODS

In drawing samples from the field, a wide strip around the edge was ignored because of the invasion of small oaks from the surrounding forest. Similarly, no samples were taken from beneath the two large hickory trees that stand isolated on the field. The depressions mentioned above were sampled separately and are not included in this report. A 60-foot trap grid had been set up on the field, and the stakes for these traps served as convenient orienting points for locating the soil samples. The location of each sample was determined by drawing a number from each of three jars, thus assuring a random distribution of samples over the field. To help the interested reader locate individual samples on the maps (Figs. 3, 5, 6), the details of the method will be given. The first drawing was for the trap at the southeast corner of a 60-foot square; the second was for a foot-wide strip running east and west within the square, starting from its northern boundary; the third was for a single square foot within this strip, starting from its western edge. Thus, the first sample on Table I, designated as B4-1450, lies in the square defined by trap positions A4, A5, B4, and B5; it is on the 14th foot-wide strip south of the line A4 - A5, and is in the 50th square foot east of the line A5 - B5.

When the square foot to be sampled had been located, the vegetation was clipped flush with the ground. A cylindrical sample 5 inches in diameter and 8.5 inches deep was taken from the center of the clipped area. The sampling device, which we are tempted to call a geotome (Schmidt, 1946), consists of a 6-inch length of 5-inch steel pipe, sharpened at one end and split lengthwise. The two halves are held together by means of a removable metal band that fits into a groove machined around the pipe. Over the top of the soil sampler is fitted a metal cap onto which has been welded a 3-foot length of 1-inch pipe. The cap serves to take the blows from a 20-pound weight of the same shape. The weight is fitted with a short length of larger pipe, which slides up and down over the 1-inch pipe as the weight is raised and dropped, driving the sampler into the ground. With this instrument it is possible to take samples from completely frozen soil. After the sampler had been driven into the ground, it was dug out, and the two halves were separated in such a way that the soil remained in one of them. The sample was then divided vertically at 1.5 and 5 inches from the surface, and the subsamples placed in coffee cans for transportation into the laboratory. Tullgren extractions were carried out by placing the soil in funnels over which were suspended 25-watt light bulbs. A series of 20 funnels enabled us to extract all subsamples simultaneously, a procedure that is greatly to be preferred to storing part of the samples while others are being extracted.

Two samples were taken each week from September 9, 1949, to September 2, 1950, with a few exceptions due to weather or scheduling difficulties. Thirty-five of the samples, taken at intervals during the entire year, have been sorted and counted; the results are given in Table I. One of these 35 samples was taken to the full depth of the soil. Three similar samples, the locations of which were arbitrarily selected close to the first, have been included with it in Table II. These three have been omitted from Table I and from the statistical aspects of the study because their selection was not random. The results from the total of 38 samples form the basis of this paper. It will be noted (Table I) that one of each pair of samples is represented by the animals extracted from the vegetation clipped from the square foot sampled, in addition to the soil fauna. Our attention has been focused upon the animals from the soil, and all of the following observations apply only to them. They are all members of the phylum Arthropoda; a few nematodes were obtained, but since the extraction method used is unsatisfactory for collecting nematodes, they have not been included.

NUMERICAL ABUNDANCE OF MICROARTHROPODS

From the 35 randomly collected samples a total of 74,572 organisms was counted. As will be shown below, about two-thirds of the extractable arthropods occur within the top 8.5 inches taken for these samples.

After making the necessary calculations, we arrived at an estimated population of 259,304 per square meter. This figure is astonishingly close to the 263,658 per square meter reported for English pasture soil by Salt, Hollick, Raw, and Brian (1948). These authors estimated that they lost enough specimens to make a total population of 351,480, which they said was minimal because of further loss of very small specimens. Their samples were taken in November, which is a time of maximal abundance of these forms. If the four November samples are considered separately, they are found to have an average of 3479 microarthropods in the top 8.5 inches of soil. This represents a total for all depths of 423,290 per square meter, a figure that is more closely comparable with that of the authors referred to above. The agreement is the more remarkable because of the different extraction methods used: Tullgren funnels in our work, and washing through a series of sieves in theirs. Such an exact agreement may be spurious because of differences between localities and extraction methods, but Macfadyen (1952), using Tullgren extractions, reported an annual average of 157,000 mites and collembolans per square meter from the top 5 cm. in Molinia tussocks in a fen. This figure is even closer to ours and that of Salt and others than it appears, as it does not include organisms from deeper levels. Macfadyen stated that the number of these varied, but that they made up an appreciable fraction of the total, especially in winter. Using his figures to make necessary additions, we arrived at estimated populations of 111,440 in October, 458,490 in February, and 250,710 in May, not including nonoribatoid mites below 5 cm.

The three areas thus support distinctly comparable numbers of microarthropods. All estimates of numbers are considerably higher than had been reported previously. This agreement among pastured areas in the temperate zone invites comparison with other areas. Comparing pastured with forested areas is difficult because there seems to be little agreement between studies in forests. Thus, Allee, Emerson, Park, Park, and Schmidt (1949) reported 2000-3500 microarthropods per square meter of leaf mold in Illinois forest, Pearse (1946) reported an average of 18,503 per square meter of leaf mold and 5 inches of soil in North Carolina, and Hoffmann, Townes, Swift, and Sailer (1949) reported 105,044 per square meter in Pennsylvania (litter plus 1 inch of humus). Since these represent a 50-fold difference, about all one can say is that the estimates are less than comparable figures for pastures in the same latitudes, not more, as is stated by Allee and others (1949: 488), although it is clear that complete soil samples from forests are needed in order to obtain the confidence that repeatability provides.

Salt (1952) compared the soil faunas of English and tropical African pastures and found that soil arthropods are about twice as numerous in the former as in the latter. E. C. Williams (1941) reported an average of 9,822 organisms per square meter in a Panama rain forest. He collected only the leaf litter and the "loose soil on the surface." Since Pearse found 55-74 per cent of his organisms in this fraction, the two figures are comparable, although the similarity may be fortuitous, considering the above-noted range of values quoted for temperate forests. In any event, the tropical area apparently has the lesser population. These observations contradict the statements in Allee, Emerson, Park, Park, and Schmidt (1949: 473, 488) that these animals are more numerous in the tropics than in more northern latitudes. Their tentative conclusions are based mostly on early work, which was, as Salt and his co-workers stated, quite erroneous as to the total population. The facts reviewed and presented above are similar to the observations reported in Sverdrup, Johnson, and Fleming (1946) that marine plankton organisms are more numerous in high than in low latitudes. In spite of the difference in abundance, however, the turnover rate may be so much higher in the tropics that there is ample compensation for the difference in the standing crop, especially in terrestrial situations.

VERTICAL DISTRIBUTION OF MICROARTHROPODS IN THE SOIL

When this study was planned, it seemed reasonable to suppose that for all practical purposes the turf alone need be considered, since previous workers were nearly unanimous in their agreement that virtually all of the microarthropods are concentrated within a short distance of the soil surface. Notable exceptions were Dowdy (1944), who found larger invertebrates distributed downward for a considerable depth, especially in winter, and Salt, Hollick, Raw, and Brian, who stated that large numbers of organisms were collected at depths between 6 and 12 inches. A study of the soil profile indicated that it would be wise to collect to the bottom of the organic soil. The depth of this layer varies from 6 to 9 inches over the upland parts of the field. Although on some grounds it would have been more reasonable to collect to the bottom of the layer wherever it occurred, the decision was made to keep sample volumes constant, and a depth of 8.5 inches was used throughout as a reasonable approximation of the total organic soil. It soon became apparent, however, that an appreciable number of the extractable organisms was in the layer from 5 to 8.5 inches deep. This meant that some animals were being missed through too shallow sampling. When the layer from 8.5 to 12 inches deep also showed considerable numbers of microarthropods, a sample (K3-6010) was undertaken that would include the whole soil profile. At a depth between 12 and 36 inches, 4-inch layers were separated as subsamples; 3-inch layers were used below 36 inches. It was found that animals could be extracted from all layers above the parent glacial drift. To judge from the four samples taken to this depth (Table II), approximately one-third of the soil arthropods occur below the standard collecting depth of 8.5 inches (Fig. 1). This fact introduces a serious bias into the data for the majority of the samples. The bias is alleviated somewhat by two facts. First, no species is confined below the 8.5-inch depth for all four complete samples; second, no species is so distributed vertically that the majority of the specimens occur below the standard collecting depth at all seasons. Only Japygid 1 has a majority of specimens below 8.5 inches in more than one of the deep samples. Thus, it seems safe to draw conclusions based on the standard samples, with a few modifications indicated by the four complete ones (see below under seasonal changes in number and distribution).

Within the top 8.5 inches of soil the great majority of species is most numerous in the turf, and they occur in diminishing numbers downward. Only 62 of the total 177 species ever show a majority of specimens below 1.5 inches, and for many of these this represents a downward migration in late winter and spring. Only 23 species are truly characteristic of the 1.5 - 8.5-inch depth throughout most of the year. Nearly all of these come to the turf in May or June.

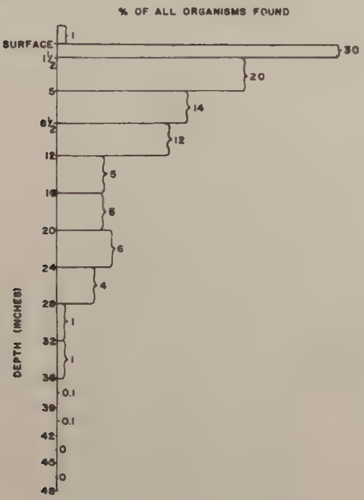


Fig. 1. Average distribution of microarthropods in a vertical transect of soil.

The finding of appreciable numbers of microarthropods at such depths is, as stated above, at variance with nearly all previous investigations. The most obvious explanation seems to lie in the physical character of the soil, which, because of its sandy nature, offers ample interstitial spaces for vertical movements. Pearse (1946) found that these animals penetrated deeper and in greater numbers in sandy soil than in clay, even though the forest was of the same type in both localities. Data on this fauna from grassy fields or meadows are, of course, not comparable with data from forests, since in the latter the soil tends to be quite shallow. Thus, the soil fauna of forests is more restricted vertically than that of grassy areas.

Before seasonal changes in numbers and vertical distribution of the soil fauna are discussed, it is necessary to consider the data as they pertain to distribution over the field and the meaning of this distribution with regard to the organization of the community.

DISTRIBUTION ON THE FIELD

When attempts were made to determine seasonal fluctuations in numbers for the various species, it became apparent that certain samples were markedly discrepant if compared with what seemed to be a seasonal trend. Thus, two samples taken in October gave lower numbers for species after species than September or November samples. It was also noted that several of the most ubiquitous species were absent from these same samples. These observations indicated the possibility that we had unwittingly taken samples from different kinds of situations and that to include observations from all in the same analysis would be unjustifiable. The sites of the different kinds of samples were not obviously different in the field, but an examination of the locations of several samples considered aberrant on the foregoing grounds indicated

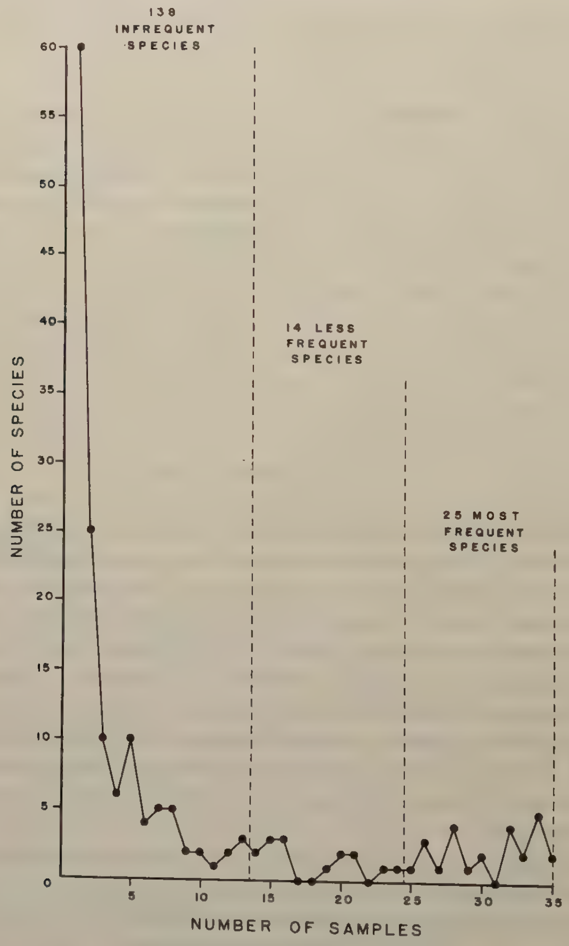


Fig. 2. Frequency of occurrence of all species of soil arthropods in 35 randomly collected samples.

that they were close to the eastern edge of the sampling area or to one of the two hickory trees on the field. Our next problem was to determine which samples represented chance variations and which fell outside such variations. Although discrepancies from seasonal trends had led us to postulate the existence of two kinds of samples, seasonal fluctuations observed for many species made the presence or absence of species more meaningful than numerical discrepancies in locating aberrant samples. The most ubiquitous species, then, should provide a stricter criterion than the most numerous ones for distinguishing between samples.

A frequency diagram (Fig. 2) of the species extracted from the soil

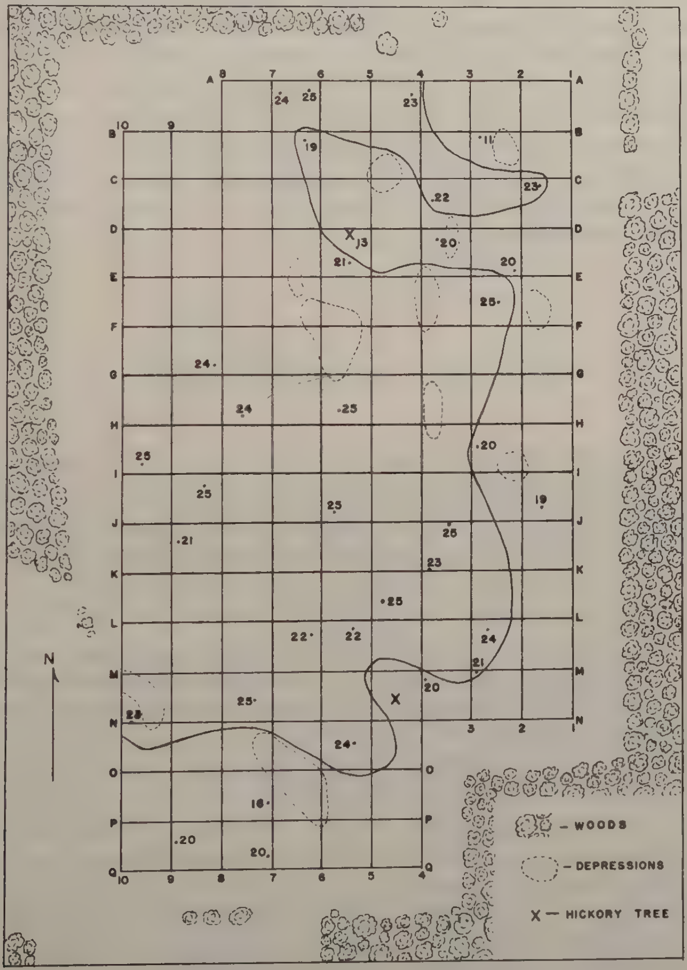


Fig. 3. Locations of 35 samples in the field and the observed number of occurrences of 25 common species in each. Grid positions are 60 feet apart.

shows an increase in numbers of species at high frequencies as compared with the number of slightly less frequent species, a situation typical of results of this kind of analysis. It will be noted that the curve begins to turn up at a frequency of about 25 samples and that there are 25 species, each of which is found in 25 or more of the 35 samples. Aside from chance absences, failures of these 25 species to appear in any sample should make one suspect that the sample came from a different kind of situation. Figure 3 is a map of the field giving the location of each sample and the number of species present from among these 25 which are most ubiquitous. It is obvious that a low number is related to the eastern and southern sides of the field and to the two large hickory trees standing on it. The line separates samples with 21 or more of the 25 species from those with 20 or fewer. It is evident, moreover, that lines separating the samples at other intervals will be nearly parallel to the line shown and also close to it. The line does divide the field into two areas; we may now consider the statistical validity of drawing it.

Among the 35 randomly collected samples there is a total of 111 failures of occurrence of one or another of the 25 species. Given this information, it is easy to calculate the expected chance distribution of absences among samples. The formulae for the successive terms of the binomial distribution are:

$$F_0 = X(\frac{X-1}{X})N; \quad F_1 = F_0\,(N)\,(\frac{1}{X-1});$$

$$F_2 = F_1(\frac{N-1}{2})\,(\frac{1}{X-1}); \quad F_3 = F_2(\frac{N-2}{3})\,(\frac{1}{X-1}); \quad \text{etc.}$$

F is the number of samples expected to have 0, 1, 2, 3, and so forth, absences; N is the total number of absences; and X is the number of samples. The results are given in Table III and Figure 4, along with the observed distributions. The same method could be used for the 764

TABLE III

Comparison of Observed and Expected Frequencies of 25 Species of Microarthropods in 35 Randomly Collected Samples

Species Present	Species Absent	Expected Samples	Observed Samples	d	d^2	d^2/e
25	0	1.44267	9			
24	1	4.66746	5			
		6.11013	14	7.88987	62.25005	10.18801
23	2	7.48166	4	3.48166	12.12196	1.62022
22	3	7.92173	3	4.92173	24.22343	3.05785
21	4	6.23250	3	3.23250	10.44906	1.67654
20	5	3.88615	6	2.11385	4.46836	1.14982
19 or fewer	6 or more	3.36783	5	1.63217	2.66398	0.79101
		d.f.: 5			chi-square:	18.48345

observed occurrences of the 25 species in the 35 samples, but the arithmetic would be more cumbersome and would yield only a mirror image of the curve obtained; we have thus equated 0 absences with 25 occurrences, 1 absence with 24 occurrences, and so forth, in Table III. There are more samples with all 25 species and more with 20 or fewer species than would be expected. When a test by chi-square at the 99 per cent confidence level is made, the probability that the observed distribution depends on chance is less than 0.003. The 99 per cent confidence limit is obtained by lumping the ends of the "expected" curve until the first expected number exceeds 2.0. The statistical test shows it to be highly improbable that the 35 samples all belong to the same group; the bimodal nature of the "observed" curve in Figure 4 confirms the foregoing suggestion that we are dealing with two kinds of samples.

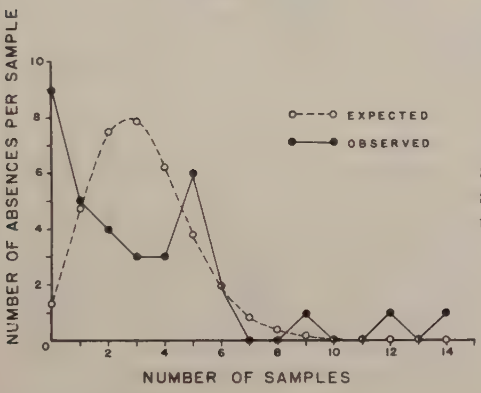


Fig. 4. Observed distribution of absences of 25 common species among 35 samples, compared with the expected chance distribution.

If the 24 samples containing 21 or more of the species are considered as a group and tested statistically in the same manner, they seem to be alike in the occurrences of the 25 species, subject to chance variations (chi-square is 4.98, with 3 degrees of freedom). The other 11 samples are distinctly different and must be discarded in considering seasonal fluctuations, vertical distribution, and mathematical relations between the numbers of species and individuals.

In spite of initial attempts to avoid the effects of the surrounding forest, the foregoing analysis indicates that we had not done so. The failure, however, seems to us to give evidence concerning the delicacy of balance of community organization. There is a large area in the center of the field where conditions are such that all of the 25 most ubiquitous species are extremely likely to occur. This area gives way abruptly to a peripheral one (not obviously different to the human observer) where conditions are such that five or more of these species are likely to be absent. We can envision only one or two factors that could produce this sharp division of the field into two areas: the effect of the shadow line of the trees at some critical season, or possibly the effect of widely spread tree roots in removing something critical from the soil. The curious feature is the absence of an obvious floristic division corresponding to this faunistic division.

One point concerning the observed division of the field that will have occurred to the critical reader is the effect of seasons upon the numerical abundance, and hence ultimately upon presence or absence, of these 25 species. In other words, are the seasons equally well represented on both sides of the line drawn in Figure 4, or is there an accidental correlation between season and distribution? To answer the question, the year was divided into four equal parts between solstices and equinoxes, and the sets of samples inside and outside the line were tested against the total distribution by means of chi-square. The results are given in Table IV. The seasonal variations in distribution of samples

TABLE IV

Comparison of the Proportions by Seasons of Samples Otherwise Classified According to the Presence or Absence of 25 Species of Soil Arthropods

Season	Total Samples	Number Inside Line	Number Outside Line					
	(P_i)		(x_i)	$\bar{p}P_i$	$x_i-\bar{p}P_i$	$(x_i-\bar{p}P_i)^2$	$\bar{p}\bar{q}P_i$	$\frac{(x_i-\bar{p}P_i)^2}{\bar{p}\bar{q}P_i}$
Fall	12	10	2	3.7716	-1.7716	3.1386	2.5862	1.2136
Winter	7	4	3	2.2001	0.7999	0.6398	1.5086	0.4241
Spring	12	6	6	3.7716	2.2284	4.9658	2.5862	1.9201
Summer	4	4	0	1.2572	-1.2572	1.5805	0.8621	1.8333

chi-square: 5.3911

$\bar{p} = 11/35$ 0.3143; $\bar{q} = 1 - \bar{p}$ d.f.:3 $0.1 < p < 0.2$

TABLE V

Comparison of the Proportions by Seasons as in Table IV

Here the seasons are of unequal length and each has approximately the same number of samples.

Dates	Total Samples	Number Inside Line	Number Outside Line					
	(P_i)		(x_i)	$\bar{p}P_i$	$x_i-\bar{p}P_i$	$(x_i-\bar{p}P_i)^2$	$\bar{p}\bar{q}P_i$	$\frac{(x_i-\bar{p}P_i)^2}{\bar{p}\bar{q}P_i}$
Sept. 22- Nov. 17	10	8	2	3.1428	-1.1428	1.3060	2.1550	0.6060
Dec. 15- March 18	9	6	3	2.8287	0.1713	0.0293	1.9396	0.0151
March 25- May 6	8	3	5	2.5144	2.4856	6.1782	1.7241	3.5834
May 27- Sept. 2	8	7	1	2.5144	-1.5144	2.2934	1.7214	1.3302

chi-square: 5.5347

$\bar{p}$ and $\bar{q}$ same as for Table 4 d.f.:3 $0.1 < p < 0.2$

are not significantly different from chance. Table IV shows the most meaningful ecological division of the samples by season. It does concentrate them in fall and spring. Dividing the samples so that each time period, regardless of length, gets a nearly equal number does not alter the statistical result, as is demonstrated in Table V.

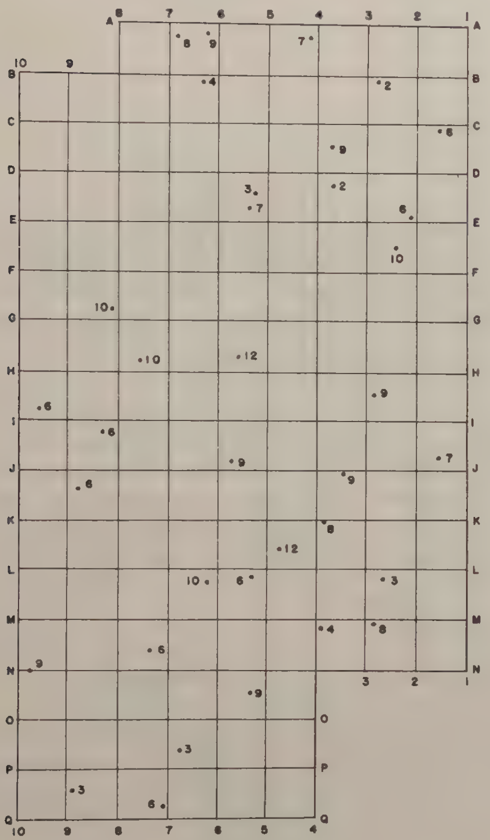


Fig. 5. Locations of 35 samples in the field and the observed number of occurrences of 14 less common species.

It thus seems justifiable to conclude that the field is divided rather sharply into two distinct areas as far as the 25 most ubiquitous species are concerned. What of the less frequent species? To return to Figure 2, there seems to be no natural division of the remaining 152 species. An arbitrary division was made into those found in 14-24 samples and those found in 1-13 samples. The number of species present in each sample for the two categories is given in Figures 5 and 6. There seems to be a general correlation between the number present of the less frequent species of both categories and the number present of the 25 most ubiquitous species. This correlation is weak, however, as is shown when the number of ubiquitous species is plotted against the number of all other species (Fig. 7). It seems clear from Figures 5, 6, and 7 that there is no sharp division of the field for the 152 species which are not among the 25 most ubiquitous. Rather, there seems to be a gradual increase in numbers of species as one approaches the center of the field, and even this trend is far from clear-cut. That the field is not divided sharply for the 14 species occurring in 14 -24 samples is shown in Table VI. The comparison is made in the same manner as that for Table III. The distribution of absences is not significantly different from chance. About all one can say is that a low number of species in the most frequent group is always accompanied by a low number of species in general. The converse is not true.

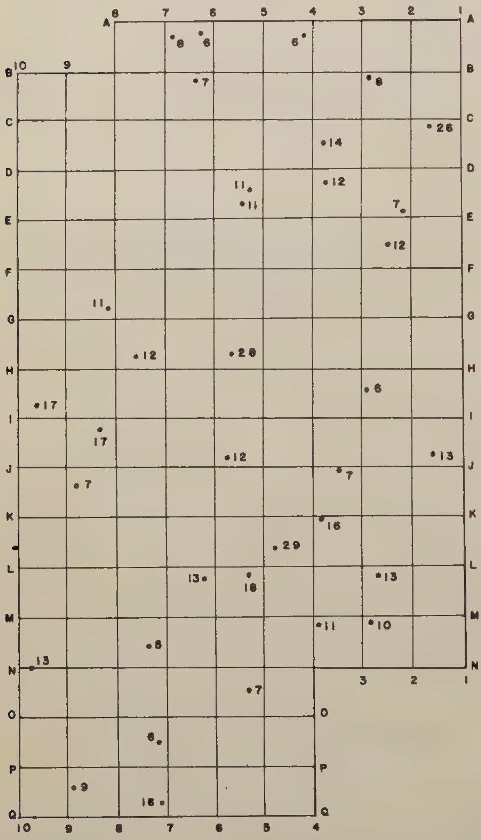


Fig. 6. Locations of 35 samples in the field and the observed number of occurrences of 138 uncommon species.

The foregoing facts seem to indicate that as far as 95 per cent of the soil fauna is concerned, a large area at the center of the field shows remarkable constancy in species composition. The remaining 5 per cent of the individuals, making up 86 per cent of the species present, lends little if anything to the characterization of the community, as is shown by their irregular presence, either as single species or as groups. The tempting conclusion, which remains to be proved, is that this large number of species is not really concerned with any community organization, and, indeed, the whole group might be considered either accidental or transient in occurrence.

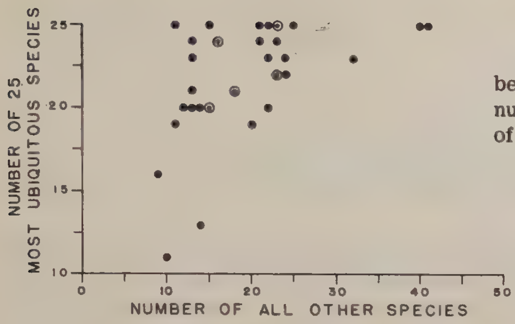


Fig. 7. Relation between the number of 25 common species and the number of all other species in each of 35 samples.

A wide strip along the eastern and southern margins of the field and surrounding the two trees is much less constant in species composition. As mentioned above, a shade line at some critical period seems the most reasonable explanation of this phenomenon, although it is difficult to explain why it should have such a marked effect upon the soil fauna, either directly or indirectly. The strip does not appear to be ecotonal in nature, as evidenced by its failure to show obvious floristic differences from the rest of the field. Moreover, ecotones are generally rich in species, not poor, as is the present case. Whatever the explanation for the existence of this strip, its clear-cut difference from the center of the field precludes the use of the 11 samples taken from it as proper representatives of the field community. In succeeding sections of this

TABLE VI

Comparison of Observed and Expected Frequencies of Absences of 14 Species of Microarthropods in 35 Randomly Collected Samples

Absences	Expected Samples	Observed Samples	d	d^2	d^2/expected
0	0.0279853	0			
1	0.202482	0			
2	0.72953	2			
3	1.74515	0			
	2.70515	2	0.70515	0.49724	0.18381
4	3.11816	4	0.88184	0.77764	0.24939
5	4.43879	7	2.56121	6.55980	1.47784
6	5.24386	3	2.24386	5.03491	0.96015
7	5.28791	3	2.28791	5.23453	0.98991
8	4.64638	8	3.35362	11.24677	2.42050
9	3.61386	0	3.61386	13.05998	3.61386
10	2.51908	2	0.51908	0.26944	0.10696
11 or more	3.42681	6	2.57319	6.62131	1.93221

d.f.:8 chi-square: 10.00242

p approximately 0.24

paper only the 24 samples from the more homogeneous center of the field will be used. The 11 excluded samples have been marked with an asterisk in Table I.

SEASONAL VARIATIONS IN NUMBERS AND VERTICAL DISTRIBUTION

Originally, it was hoped that data on seasonal variations in abundance of different species would yield information useful in attacking the problem of competition between species and ultimately the more general one of maintenance of balance in the community. Viewed from this standpoint, the results are disappointing. The variations in space are almost as conspicuous as those in time and are at least equally valuable in interpreting the community. Twenty-three of 40 species for which adequate data are available show peaks of abundance from November through

TABLE VII

Distribution of Maximum and Minimum Numbers
of Common Species of Microarthropods by Date and Sample

Fractions in the "minimum" column reflect ties between samples. Fifteen species were omitted from this column because of multiple ties between samples.

Date	Sample	Species Reaching Maximum	Species Reaching Minimum
Sept. 22, 1949	B4-1450	2	0.4
	D3-2515	0	0.7
Oct. 20, 1949	D1-0623	0	3.4
	E5-3939	1	3.73
Nov. 3, 1949	L4-3616	4	0.0
	M5-1142	0	1.7
Nov. 17, 1949	K3-6010	12	1.0
	M2-1020	0	1.4
Dec. 15, 1949	H7-4526	0	0.0
	F2-2932	2	0.0
Jan. 5, 1950	J8-1142	3	0.5
	M6-1251	1	2.2
Jan. 19, 1950	05-2841	1	1.4
Feb. 18, 1950	H5-4022	0	0.2
Apr. 8, 1950	B6-1410	2	0.7
Apr. 15, 1950	K8-2213	1	4.0
May 6, 1950	B6-1143	2	1.0
May 27, 1950	J5-4616	0	0.0
	I9-4628	0	0.0
June 10, 1950	N7-3742	1	1.0
July 15, 1950	N9-6018	2	0.3
	N2-0310	1	0.3
Sept. 2, 1950	K3-0335	2	0.0
	G8-4853	3	0.0

January (Table VII). The total microarthropod population reflects this trend (Fig. 8). The high point in April is due entirely to an exceptionally high peak in a single species, mite 09. This observation is in agreement with many studies (Macfadyen, 1952) and indicates that these species can continue to multiply at decreasing temperatures until the ground is frozen, or at least that their eggs are able to hatch under these conditions. Once the soil has been frozen for some time, however, nearly all species decline in numbers through the remainder of the winter and do not begin to recover until May or June. Minima occur least frequently in December, September, and February. October has the highest number of species reaching their minimum, followed by April and January. The October minimum occurred in marginal samples (for locations of samples in Table VII, see Fig. 3).

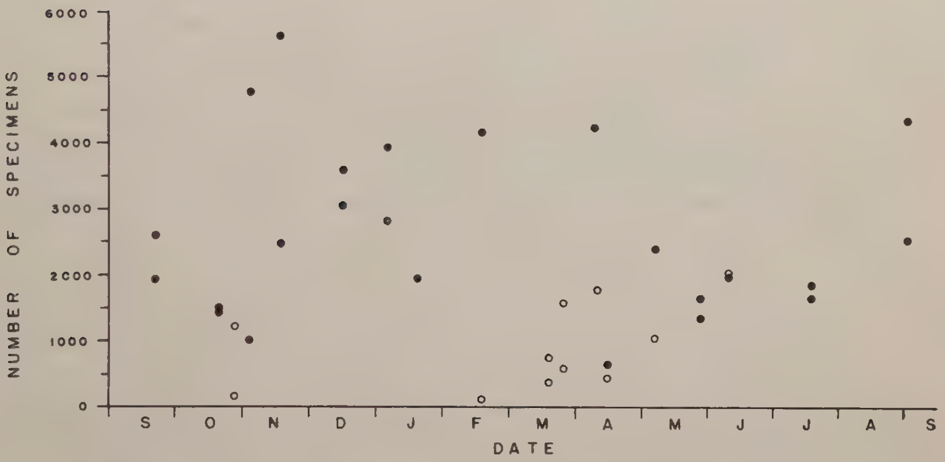


Fig. 8. Seasonal fluctuations in the total microarthropod population. Solid circles represent the 24 samples from the center of the field; open circles represent 11 samples from the edges of the sampled area.

Figures 9 and 10 show examples of species reaching seasonal maxima in late fall or early winter. It seems clear that in such cases soil moisture is of greater importance than temperature as a factor controlling abundance (see Tables VIII and IX). Unfortunately, observations on soil moisture were only begun in January, and comparisons are not available for the preceding autumn. The general correspondence of moisture with abundance of soil arthropods from January through the following autumn cannot be denied, especially when it is remembered that the high moisture contained in the soil in February and March is unavailable because it is frozen. This gives the correspondence a false appearance of a time lag.

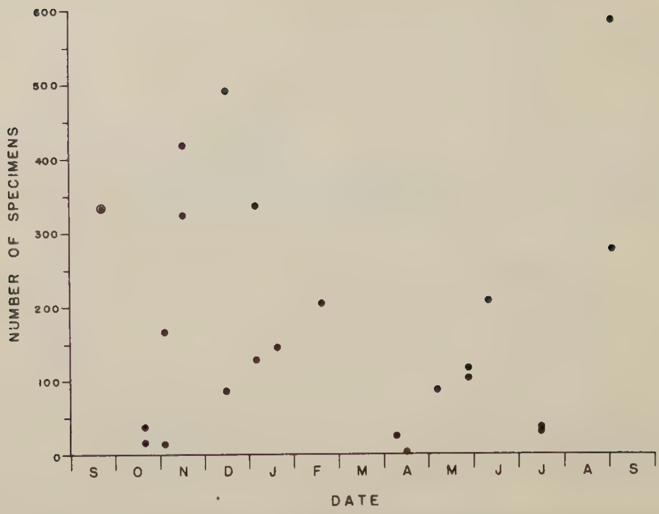


Fig. 9. Seasonal fluctuations in numbers of mite P1, showing peak in late fall and winter.

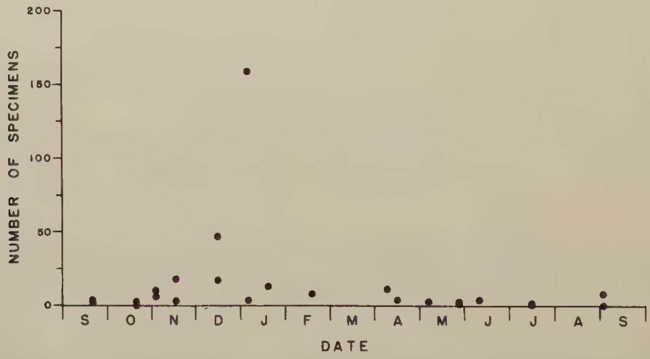


Fig. 10. Seasonal fluctuations in numbers of collembolan P5, showing peak in early winter.

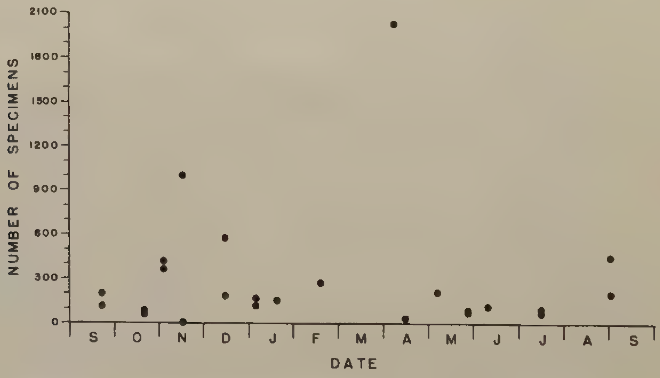


Fig. 11. Seasonal fluctuations in numbers of mite 09, showing peak in spring.

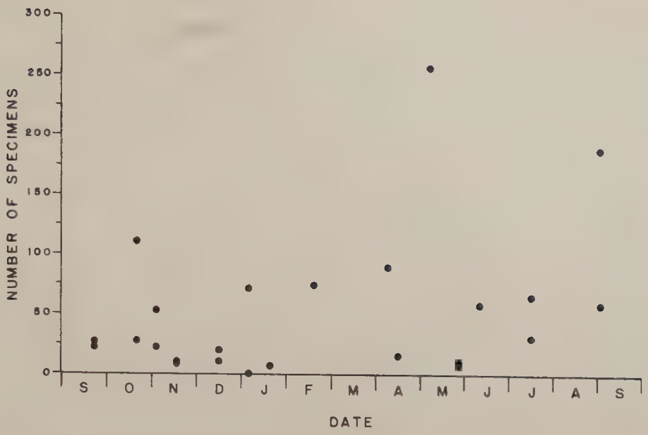


Fig. 12. Seasonal fluctuations in numbers of mite E8, showing peak in spring.

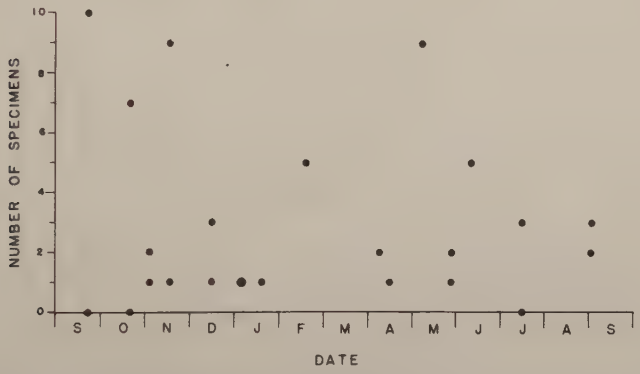


Fig. 13. Seasonal fluctuations in numbers of mite P5, a species that has no discernible peak.

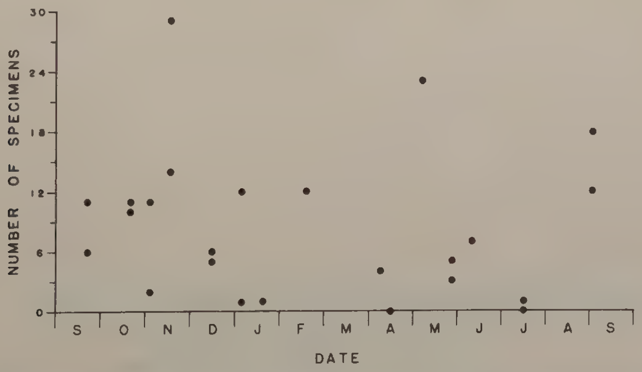


Fig. 14. Seasonal fluctuations in numbers of Protura 1, a species that has no discernible peak.

Some numerically important species do not show the foregoing pattern of a fall high and spring low. Mites 09 and E8 (Figs. 11, 12) have peaks of abundance in the spring, and several among the 25 most ubiquitous species apparently have no particular season of maximum abundance (Figs. 13, 14).

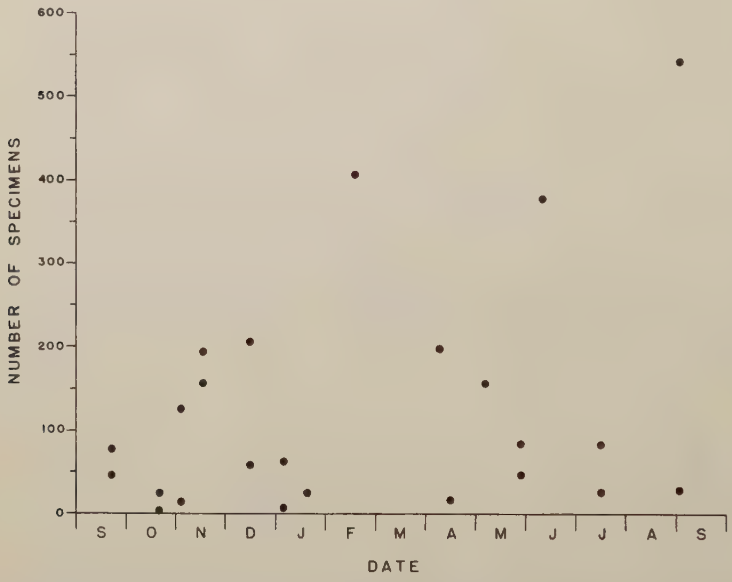


Fig. 15. Seasonal fluctuations in numbers of mite 05, showing a continuous rise during the year of observation.

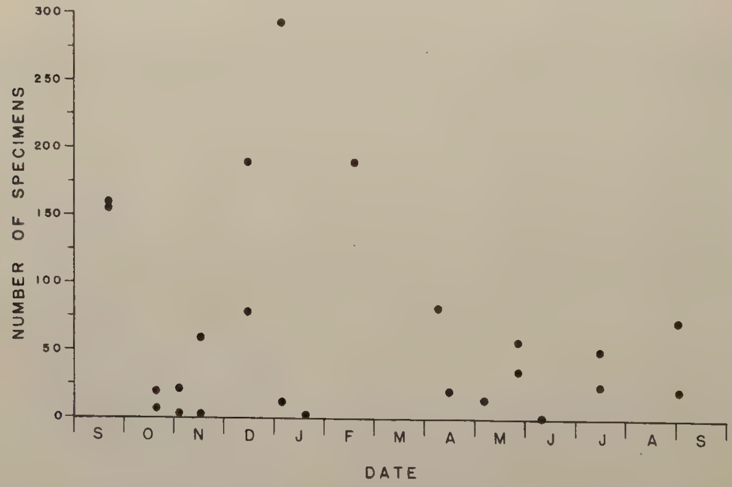


Fig. 16. Seasonal fluctuations in numbers of mite 08, showing a continuous fall during the year of observation.

TABLE VIII

Soil Temperatures at Two Depths

All readings Fahrenheit.

Depth in Inches	September			October				November			December				
	9	15	22	6	13	20	27	3	10	17	1	8	15	22	29
1.5	63	59.5	64	60	59	66	51	43	51	44	32	32	28	44	33
8.5	61	61	62	59	58	58	49	46	48	45	36	35	34	43	36
Frozen Soil												1.5	2.5		

Depth in Inches	January				February				March		
	5	12	19	25	1	11	18	25	4	15	25
1.5	33	32	26	36	32	33	32	31	31	33	36
8.5	38	34	32	33	33	34	33	33	32	32	33
Frozen Soil		1.5	8	5	4	4	3	3	8	8.5	8

Depth in Inches	April				May				June		
	8	15	22	29	6	13	20	27	3	10	24
1.5	44	39.5	49	50	58	61	69	60	61	78	81
8.5	40	36	42	45	55	56	61	61	62	68	72

Depth in Inches	July					August				September
	1	8	15	22	29	5	12	19	26	2
1.5	71	78	75	72	87	85	77	71	74	68
8.5	66	72	73	68	74	74	67	69	72	68

Of considerable interest are species that show continuous rise or fall over the year (Figs. 15, 16). Whatever the unknown factors that control them, such species are less affected by immediate weather changes than are those having an identifiable annual cycle in numbers. In these cases it is clear that a reasonable understanding of populations will come only after studies have continued over a period of years.

Many species of microarthropods do not remain at the same level in the soil throughout the year; this is especially true of those characteristic of the layers below the turf. All of these species show a movement to the turf in spring and early summer. Figures 17-20 show typical and extreme cases of the vertical movement of the bulk of the population. Each species shows a downward movement, usually beginning in July, that is often more gradual than the upward trend.

The migration into the turf is probably stimulated by temperature changes, since it begins at about the time when the soil temperature gradient is being reversed. The temperature reversal occurred during the last week in March, preceding the observed upward migration by one to three weeks (Table VIII). The spring thaw accompanied the temperature reversal, of course, and the water thus freed may have been a factor in initiating some of the migration. Table VIII shows the occurrence and depth of frozen soil. Temperature may also provide the stimulus for the return of these species to the deeper levels, although the downward migration begins before summer temperature maxima are reached. It seems at least as likely, moreover, that the increasing dryness of the summer, especially in the turf, is responsible for the descent, but the case for soil moisture is not unequivocal, as it drops more or less regularly throughout both upward and downward migrations (Table IX). Strickland (1947) attributed the annual migration that he found in Trinidad to changes in rainfall and humidity.

The reason for these migrations is not clear. One more or less automatically expects seasonal migrations to be associated with reproduction, but in the present case there seems to be no relation between the presence or absence of vertical migration and the presence or absence of any kind of seasonal cycle in numbers. Of 15 species showing fall or winter peaks in numbers, seven have an identifiable migration and eight do not; of eight species having no clear cycle in numbers, four migrate and four do not.

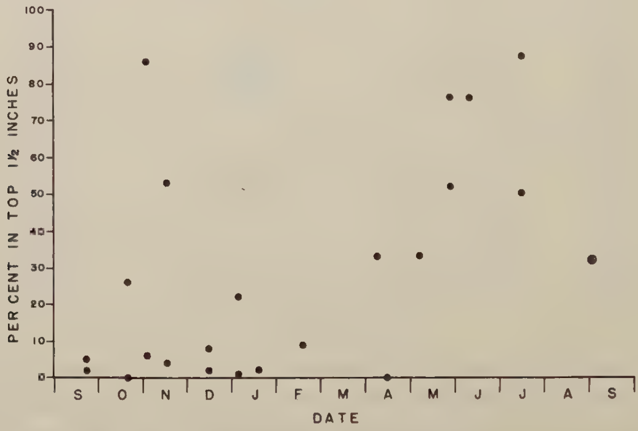


Fig. 17. Vertical migration of mite P1 in the soil.

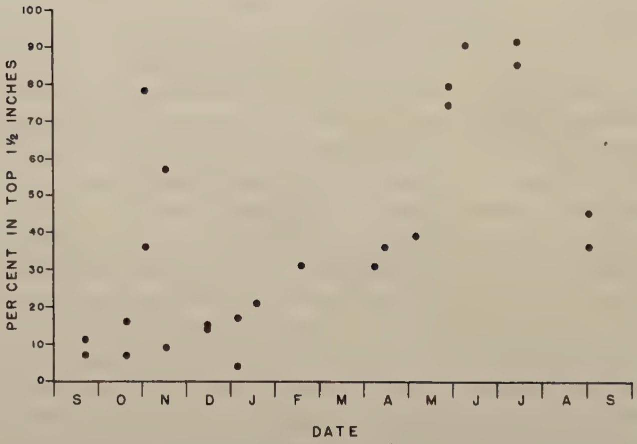


Fig. 18. Vertical migration of mite 01 in the soil.

For eight species the migration carries enough individuals below the standard collecting depth to create a false impression as to numerical abundance. The most striking example of this is Japygid 1. To judge from the standard samples, this species appears to have two peaks of abundance, a low one in November and a much higher one in June (Fig. 21). When the figures from the four complete samples are examined

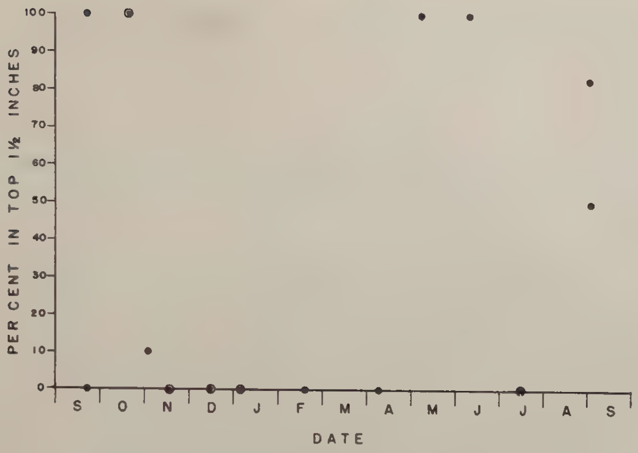


Fig. 19. Vertical migration of Protura 2 in the soil.

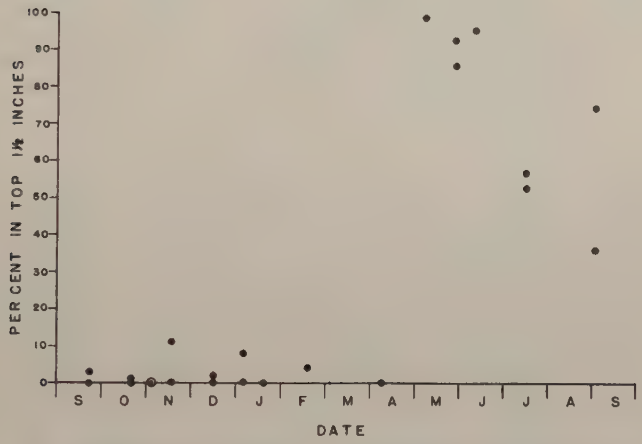


Fig. 20. Vertical migration of collembolan P1 in the soil.

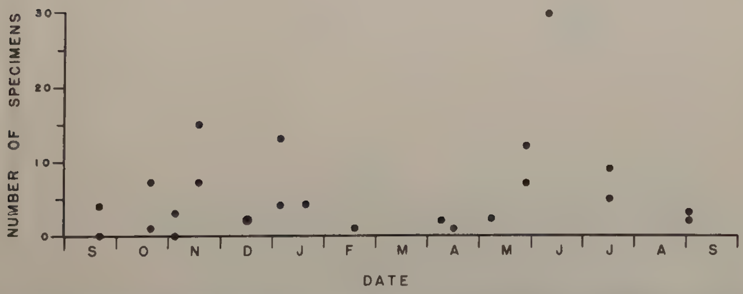


Fig. 21. Seasonal fluctuations in numbers of Japygid 1 in the top 8.5 inches of soil. Note two well-defined peaks.

TABLE IX

Soil Moisture at Three Depths, January 25 - September 2, 1950

(In per cent of wet weight.)

Depth in Inches	January	February				March		
	25	1	11	18	25	4	18	25
0 - 1.5	20.8 22.4	22.9 21.5	28.3	25.7 28.9	34.8	38.5	32.2 36.8	21.5 28.8
1.5 - 5	15.6 16.5	9.7 18.7	16.6	15.1 12.5	12.8	25.1	16.8 19.6	18.9 19.4
5 - 8.5	12.4 11.4	6.5 8.7	8.4	9.0 7.7	9.6	10.6	12.7 11.9	11.1 10.2

Depth in Inches	April				May			
	8	15	22	29	6	13	20	27
0 - 1.5	26.0 13.5	13.1 8.5	13.2	12.3 10.8	11.3 7.8	8.3 9.8	5.1	12.2 11.3
1.5 - 5	8.8 10.6	10.3 6.4	9.9	9.3 8.6	8.1 6.1	8.2 8.0	2.9 5.4	9.9 9.6
5 - 8.5	7.5 10.5	9.3 6.2	9.6	9.3 7.7	8.7 6.3	7.7 7.4	2.6 8.3	10.0 9.5

Depth in Inches	June			July				
	2	10	24	1	8	15	22	29
0 - 1.5	11.9 10.3	11.7 7.9	20.8 9.5	6.7 8.7	4.8 5.2	3.5 2.3	10.3 9.3	3.7 2.9
1.5 - 5	10.6 9.0	6.6 6.6	9.4 9.4	5.7 7.6	5.8 6.0	4.6 3.3	8.2 8.7	4.3 5.3
5 - 8.5	10.3 9.1	6.1 7.0	9.4 8.7	6.0 7.2	5.8 5.7	5.9 3.9	8.0 9.1	4.8 6.2

Depth in Inches	August				September
	5	12	19	26	2
0 - 1.5	2.0 2.1	10.0	7.5 5.5	3.9 2.6	9.5 8.4
1.5 - 5	3.9 2.2	8.7	6.4 5.2	4.5 4.1	7.8 7.3
5 - 8.5	4.6 2.8	8.7	6.0 5.4	5.3 4.5	6.9 6.5

(Table II) and considered in conjunction with the data on vertical distribution, an entirely different concept of the seasonal abundance is obtained (Fig. 22). There is only one peak of abundance, which comes in November. The early summer "peak" is apparently due entirely to the appearance in the upper five inches of a number of specimens that have been below the standard collecting depth and have been missed in all samples except the deep ones of November, February, and April. We believe that the migrational phenomenon involved here is the explanation for the two peaks found for several species by Strenzke (1951) since his

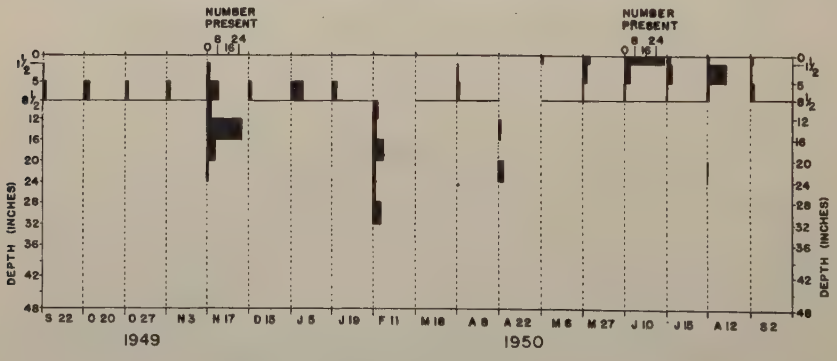


Fig. 22. Vertical distribution of Japygid 1 in all samples, including 4 deep ones. Note effect of vertical movements on apparent abundance in top 8.5 inches.

findings are at variance with the results of most other studies (Macfadyen, 1952). Dowdy (1944) has described vertical movements of this sort for macroscopic invertebrates, but they were mostly sharp descents in January with a quick return to the upper layers. Other similar findings are cited by Macfadyen.

RELATIONSHIP BETWEEN NUMBERS OF INDIVIDUALS AND OF SPECIES

Since the community concept began to take form, there have been attempts to find some constant numerical relationship between the species in a community. Earlier attempts (Raunkiaer and others) centered on the frequency of occurrence of various species. More recently, use has been made of numerical abundance rather than frequency. These later analyses have been based largely upon groups of species that were related taxonomically (moths in a light trap, birds in a valley) rather than upon species that might be presumed to be related ecologically. The same criticism holds to a certain extent for the present study, as the collecting technique is worthless for organisms other than microarthropods. The animals concerned were removed from known volumes of soil, however, and were not drawn in from surrounding and ecologically divergent territory. Since they came from the same place, they may be assumed to have some ecological relationship to one another (Dice, 1952: 15).

There can be no doubt of the value of a system that will describe mathematically the relationship between the number of species and the number of individuals in a natural situation. Two uses of such a system may be mentioned: One would be a completely unbiased method for comparing different localities in terms of general biotic composition; the other would be that with an adequate (and possible) sample, an accurate prediction could be made of the total number of species in a biological universe, to borrow Preston's term (1948). Our data lend themselves readily to such an analysis. Indeed, we have used a modification of the Raunkiaer curve in analyzing the distribution of organisms on the field. This curve, however, is generally recognized to be of little value in comparing samples of different sizes and does not properly allow for species with strongly clumped distributions. Both the logarithmic series, devised by Fisher and Williams, and the lognormal curve, applied by Preston, take into account the numerical abundance of each species. The results of analyzing our data by these two methods may now be considered.[1]

---

[1] If the papers of Williams (1953) and Brian (1953) had been available at the time of writing, this section of our paper would have taken a different form, but the conclusions would not be altered. Williams concedes that the logarithmic series is less useful than the lognormal. Concerning Brian's contention that the form of the curve is nearer to the negative binomial than to the lognormal, we agree that this is probably true, but the difficulty presented by the nonconformity of samples of different sizes (Fig. 24) remains. This nonconformity is also evident, though less conspicuous, in Williams' chart of light-trap data (loc. cit., p. 23).

Logarithmic Series

Fisher, Corbet, and Williams (1943) presented a mathematical analysis of data involving a collection of Malayan butterflies, and of Lepidoptera caught in a light trap at Harpenden, England. They found that the relation between the number of species and the number of individuals could be expressed by the following equation:

$$S = \alpha \log_e(1+\frac{N}{\alpha})$$

In this equation S is the number of species in the sample, N, the number of individuals, and alpha is a constant that is most easily obtained from Fisher's table (1943). The constant alpha represents an index of diver-

TABLE X

The Index of Diversity (Alpha) for Samples of Three Different Sizes Obtained by Lumping Randomly Drawn Pairs, Groups of Five, and Groups of Twelve Single Samples

	Sample	Date	Species in Group	Individuals in Group	Alpha for Group
Pair 1	J8-1142	Jan. 5, '50			
	M5-1142	Nov. 3, '49	64	4,999	10.3464
Pair 2	N2-0310	July 17. '50			
	05-2841	Jan. 19, '50	52	3,661	8.584
Pair 3	K3-6010	Nov. 17, '49			
	K3-0335	Sept. 2, '50	59	8,197	8.537
Pair 4	M5-1142	Nov. 3, '49			
	D1-0623	Oct. 20, '49	71	2,529	13.568
Pair 5	J5-4616	May 27, '50			
	K8-2213	Apr. 15, '50	53	2,326	9.659
Ave. value for 5 pairs					10.139
Group 1	K8-2213	Apr. 15, '50			
	B6-1143	May 6, '50			
	N2-0310	July 17, '50	92	12,880	13.424
	M2-1020	Nov. 17, '49			
	K3-6010	Nov. 17, '49			
Group 2	K3-6010	Nov. 17, '49			
	05-2841	Jan. 19, '50			
	K3-0335	Sept. 2, '50	86	15,948	11.955
	G8-4853	Sept. 2, '50			
	I9-4628	May 27, '50			
Ave. value for 2 groups					12.690
Group 1	(alternate samples, beginning with B4-1450 in Table I; samples marked with asterisk omitted.)		123	34,056	16.0679
Group 2	(alternate samples, beginning with D3-2515 in Table I.)		124	30,178	16.5205
Ave. value for 2 groups					16.3621

sity; a large value indicates a large number of species in relation to the number of individuals and hence a greater diversity in the biota. Perhaps the greatest advantage claimed was that the value of alpha remained constant for any adequate sample drawn from the same population of species. Thus, the biota (or any comparable parts) from different localities could be compared in a convenient objective manner. The value of alpha, therefore, was calculated for each of our samples. The values ranged from 5.42 to 11.36, with a mean of 7.89. They showed no seasonal trend, and although the mean for the 24 samples in the center of the field (see above) was higher than for the 11 samples more or less peripheral in location, the difference was not significant. When the 24 samples were lumped and considered as a single sample, however, the value of alpha was 19.315, or more than twice the mean value for individual samples. On further analysis it was found that pairs of samples, drawn at random from the group of 24, gave an average of 10.139; groups of 5 samples, an average of 12.69; and groups of 12, an average value of alpha of 16.36 (Table X). Thus, for our samples the value of the constant is clearly related to the size of the sample. In fact, this relationship is remarkably close to a straight line on a log-log plot of alpha against sample size (Fig. 23). In view of the claims of Fisher, Corbet, and Williams, this finding is unexpected, and only two explanations seem tenable at present:

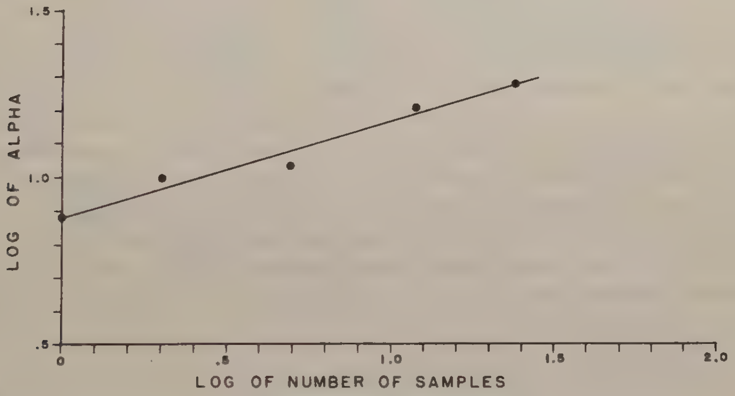


Fig. 23. Relation between the index of diversity and sample size.

(1) The community being sampled is found to be increasingly heterogeneous as larger and larger samples are drawn from it, that is, new species are added relatively faster than new individuals; (2) the formula employed does not properly express the relationship in question. Since the 24 samples used were deliberately selected for uniformity of species composition, the second alternative seems the more likely. In an effort to obtain further evidence, the following analyses were performed:

1. The two pairs of samples taken closest together in both space and time were selected as the pairs most likely to show the greatest uniformity of faunal composition. Accordingly, if the fact that increasing the

number of samples raises alpha is a reflection of the increasing distance between samples in space and time, these two pairs should give lower values of alpha than pairs selected at random. Such, however, is not the case. Two samples taken August 12 and September 2, 1950, on the same 60-foot square (K3) gave a value of 10.61 when lumped together, and a pair taken November 3, 1949, on adjacent squares L4 and M5 gave a value of 13.12 when combined. These two values of alpha are above the average for randomly combined pairs, although both are within the total variation of such pairs (Table X). The hypothesis that the field shows more and more heterogeneity with increasing sampling is not confirmed by the foregoing observation.

2. A second approach toward more homogeneous material was to consider only the species characteristic of the soil below the turf in the 24 samples. The turf constitutes a barrier against any stray individuals from other communities. One might thus be reasonably certain that practically all organisms collected below this stratum would be true constituents of the field community. An increase in the size of the sample should not affect the relationship between numbers and individuals as long as the samples are drawn from the central part of the field. If the logarithmic series were a true approximation of the relationship between species and individuals, the value of alpha should be the same for large and small samples. The values for this constant are lower for the soil below the turf than for the total soil, since few species occur below 1.5 inches, and these occur in large numbers. The average sample gave an alpha of 2.82; the 24 samples lumped gave an alpha of 3.87. The difference between these two figures is greater than it should be, since for samples of this size the error of alpha should be between 5 and 10 per cent (Fisher, Corbet, and Williams, 1943). Again, the index of diversity is directly related to sample size, and we reject the hypothesis that the relationship is due to increasing heterogeneity.

It is worth noting that these comments were written prior to the publication of the analysis of Myers and Chapman (1953), who found that the logarithmic series had no practical application to the plant community that they studied.

Lognormal Distribution

In discussing the logarithmic series Preston (1948) pointed out that this method assumes that the lowest category (the number of species represented by one individual) is the most numerous regardless of sample size. Carried to its extreme, with the world biota as a sample, this assumption is of course preposterous. There must be relatively few species so close to extinction. On a smaller basis it remains a possibility, as strays may make up a sizable fraction of the species present in many samples. We agree with Preston, however, that in a biological universe extremely rare species are probably comparable in numbers to the extremely abundant ones and that most species are intermediate in numerical representation. Preston concluded that the relations are adequately described by a Gaussian curve, when the ordinate is on a scale of $\log_2$. Thus, doubling the sample size moves the curve one unit to the right and reveals a larger fraction of the same curve. The formula for this curve is:

$$S_r = S_o e^{-(ar)^2}$$

S_o is the number of species at the mode of the curve (maximum number of species represented numerically between any successive powers of 2); these spans of numbers between successive powers of 2, the units on the ordinate, are called octaves. Thus, S_o is the number of species in the modal octave; S_r is the number of species r octaves from the mode; e is the base of natural logarithms; a is a constant. After applying this formula to a number of biological universes, Preston concluded that the constant a is nearly always close to 0.2 and that the mode of the curve usually falls within a few octaves of 2^5 individuals for relatively complete data.

The application of this type of analysis demands very large samples, since the height of the mode is determinable only by observation, and at least one octave below the modal octave must be observed before the mode can be located with any confidence. In our data only the organisms below the turf yielded a sufficiently large number of individuals in relation to the number of species. Upon plotting the total number of organisms below 1.5 inches (Fig. 24), we find a reasonably good fit with the lognormal curve for $S_o = 4$; $a = 0.16$. According to expectations, then, the average sample would follow the same curve, starting 4.5 octaves to the right of the total curve, since the average represents 1/24 of the number of individuals of the total. That such is not the case can be seen in Figure 24. Again, a reasonable fit to a lognormal curve exists, but the two curves do not coincide. It should be emphasized that an increase in sample size moves the mode of the curve up and to the left. Since the area under the curve represents the number of species present, it is

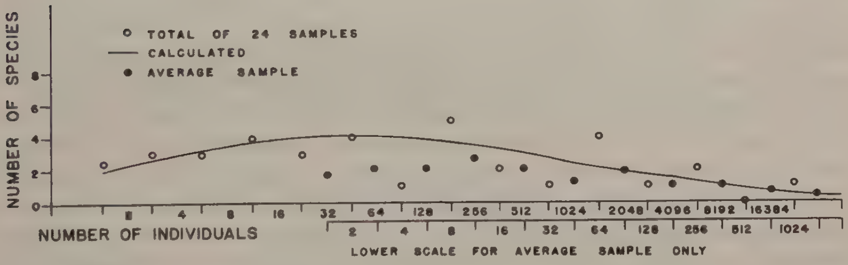


Fig. 24. Application of the lognormal curve to the total population below 1.5 inches in 24 samples and to the average of these samples.

clear that increasing the sample size has increased the apparent heterogeneity of the field. The lognormal curve, then, also fails to describe the relation between individuals and species for samples of different sizes. This is the test that any mathematical system must pass, if it is to be useful to ecologists, and no such system is forthcoming as yet. A little reflection will suffice to show why the devising of such a system is likely to be unrewarding. In all of these mathematical systems it is assumed that one curve will describe the cumulative distributions of individual species, a situation that could obtain only if all of the species involved had the same kind of distribution. Individuals of different species are not distributed in the same manner in space. To take extreme examples, ants have a strongly "clumped" distribution, while many birds, because of their territoriality, have a nearly even distribution within suitable habitats. To add the two distributions is not valid, although doubtless some sort of curve could be drawn that would describe the situation mathematically.

We may now consider why an increase in sample size apparently increases the heterogeneity of a biological universe, even within the same universe. If, in general, the most numerous species are those with a more or less random distribution, or if they are sufficiently numerous that any clumping does not result in their absence from a large number of samples, then an increase in the number of samples will not have any effect upon a curve describing their distribution. With rarer species, however, clumping becomes an important factor as the curve expands. If the rare species are strongly clumped, adding samples will be more likely to add new species rather than individuals of species already recorded. With the total number of individuals increasing at an approximately even rate, the fauna will appear to become more diversified because of this effect of the clumping of rare species. It is easy, though somewhat tedious, to estimate the degree of clumping for reasonably abundant species (those occurring in more than half of the samples). It is most conveniently done by applying the negative binomial distribution (Anscombe, 1949). The value of the constant k decreases as the degree of clumping increases and in the logarithmic series assumes a value of 0. As an example of the application of the negative binomial in a species that shows neither random distribution nor extreme clumping, Protura 2 has been selected. In this case k has a value of 0.915. Comparing the theoretical with the observed distribution (Table XI), we find a satisfactory agreement; chi-square is 4.79 with 6 degrees of freedom at the 95 per cent confidence limit. Unfortunately, the value of k cannot be estimated with any reasonable confidence for the rare species, and hence no comparison can be drawn with more abundant ones. It can, however, be demonstrated that many of these rare species are clumped and without recourse to complex statistical manipulations. Of the 38 species represented by a total of 2, 3, 4, or 5 specimens each, 13 (slightly over one-third) have the most strongly clumped distribution possible, with all specimens in one sample out of 24 (Table XII). In addition, the table shows that fewer than half of the species have the most probable distribution, based on an assumption of randomness. Although only the species

TABLE XI

Application of the Negative Binomial Distribution to the Observed Distribution of a Species of Protura in 24 Soil Samples

Number per Sample	Observed Samples	Expected Samples	Difference Squared / Expected Samples
0	7	7.116	0.00189
1	4	4.7868	0.1293
2	4	3.3695	0.11798
3	5	2.40697	2.79347
4	1	1.73193	0.30932
5	0	1.2516	1.2516
6 plus	3	2.3372	0.18976
	d.f.:6	chi-square:	4.79152

represented by a total of 2-5 specimens are included in Table XII, a perusal of Table I will serve to confirm the marked clumping of the infrequent species. Of course, nothing can be said of the 45 species represented by one specimen each.

We consider that the foregoing facts adequately support our hypothesis that the less common species are sufficiently clumped to give the impression of an increasing heterogeneity with increasing sample size, when all species are treated on a single distribution curve.

The easiest curve of this sort to understand is the "species-area" curve, widely used by plant ecologists. Applied on an arithmetical scale, this curve appears to be approaching an asymptote at about 38-40 species for soil arthropods below the turf (Fig. 25). On a scale using logarithms of the sample size, the relationship is apparently a straight line, with no hint of a bend at either end (Fig. 26). An extrapolation downward predicts a sample containing no species at a size between 1/16 and 1/32 of the standard sample, but the minimum number of

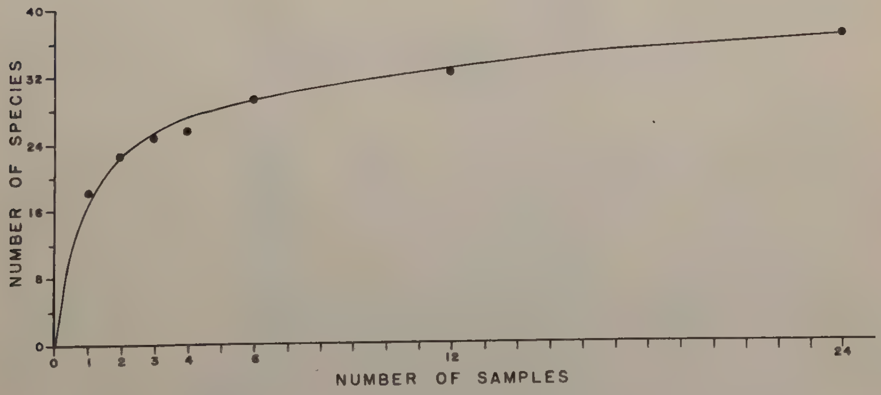


Fig. 25. Species-area curve for soil arthropods below 1.5 inches.

TABLE XII

The Distribution of 38 Rare Species of Soil Arthropods in 24 Samples

Individuals Per Species	Species	All Specimens Separate	Species Having These Distributions								All Specimens in One Sample
			1-2	1-1-2	1-1-1-2	1-3	1-1-3	2-2	2-3	1-4	
2	21	12*	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	9
3	4	2*	2	. . .	. . .	. . .	. . .	. . .	. . .	. . .	0
4	6	0*	. . .	2	. . .	0	. . .	1	. . .	. . .	3
5	7	0*	. . .	. . .	2*	. . .	2	. . .	0	2	1

*Most probable distribution, assuming randomness; the two distributions marked for 5 specimens have an approximately equal probability.

individuals below the turf in any of the 24 samples is 152, and the mean number is 1333.5. Thus, the most probable size of a sample that would be expected to be negative could hardly be larger than 1/152 - 1/1300 of the standard, and therefore the curve must bend to the left at its lower end, as suggested in Figure 26.

Must it also bend to the right to give an upper asymptote, as Preston states? Only observation can answer the question, of course, but logic suggests that the curve should flatten before the limit of the community is reached. In any case, the point of its bend must be found, or the entire community must be counted before one can devise a satisfactory mathematical system to describe the relationship between the number of species and of individuals. In the case of the community under consideration, a search for the upper asymptote seems impractical. Perhaps less complex communities could be found in which such an approach would be feasible. If so, this would be a fruitful field for investigation.

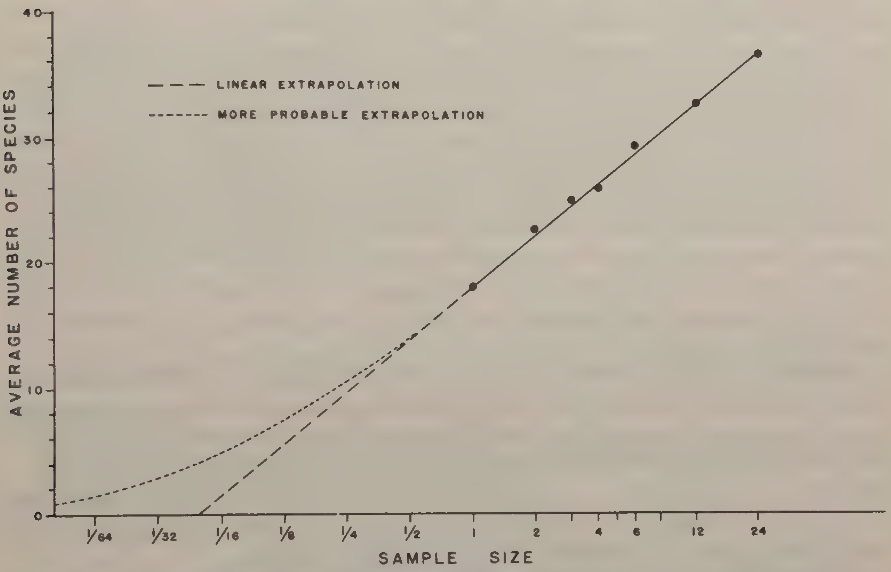


Fig. 26. Species-area curve for soil arthropods below 1.5 inches, with the ordinate in logarithms of sample size. Two theoretical extrapolations.

It is not surprising that the less common species should be clumped in any natural community. The very fact of their rarity suggests that conditions are not suitable for them everywhere in the community, either in space or in time. In a randomly drawn set of small samples it is not unreasonable to suppose that suitable conditions for such a species would be encountered infrequently, or not at all. Moreover, different samples would be likely to contain suitable conditions for different rare species. On this view, the more abundant species would be those finding conditions more or less favorable over much or all of the community or of a particular stratum. This supposition regarding the difference in status between common and rare species is confirmed in the present study in the distribution of the 25 most ubiquitous species, where absences of different species are correlated, indicating a major change in over-all conditions in the soil.

SUMMARY AND CONCLUSIONS

As an approach to the complex problem of analyzing a natural community, the small arthropods of the soil of an abandoned field were sampled over a period of one year. Admittedly a small segment of the community, they nevertheless provided ample complexity, as attested by the fact that 74,572 were counted from 35 soil samples. This rather staggering total contains 177 kinds, not taxonomically identified, but assumed to be equatable with species. The individuals are distributed among the species in such a fashion that the 25 species found in 25 or more samples account for 95 per cent of the specimens. There is evidence that these 25 species may form an ecologically closely interrelated group. For any sample there is a strong tendency for all or nearly all to be present, or for five or more to be absent. The samples with the complete set of 25 species occupy the center of the field; those lacking five or more are related to the sides of the field and to the two large hickory trees on it. We consider that the peripheral area, which is not obviously different from the center, has conditions sufficiently different to upset the ecological relationships among these 25 species and to preclude the use of the 11 samples taken from it. The larger central area is evidently more homogeneous as far as 95 per cent of the microarthropods are concerned.

Within the central area, the microarthropods are most abundant in the turf but occur as deep as 39-42 inches in the soil. Seasonal maxima occur typically in late fall or early winter, with minima in April, although there are exceptions. Many species have a vertical migration, the bulk of the population moving upwards in April or May and descending in July or August. Moisture and temperature are interrelated with both fluctuations in numbers and vertical movements.

The uniformity of the center of the field for the relatively few ubiquitous and common species is emphasized in a consideration of mathematical analysis of the relationships between species and individuals. Because results of these analyses are all related to sample size, none is of value in interpreting the community. The reason for their failure is illuminating, however. The clumping of the rare species causes each system to reveal an increasingly heterogeneous community as sample size is enlarged, or as new samples are added. This is because new species are more likely to be added than more specimens of species already found. Thus, the mathematical models fail to represent the community accurately, but the clumping of the rare species shows that the community is far from uniform for them.

Once again, then, there emerges a clear difference between the

common species and the rare ones. The former, by their ubiquity and abundance, characterize the community and give it a fundamental unity that is obscured by the large number of rare species, each of which may find suitable conditions in only a few restricted places in the community. The less common species of microarthropods, then, would be quite similar to the less common species of plants, which are also clumped in distribution and which, because they are conspicuous, have attracted considerable attention to the "mosaic" nature of the community (Evans and Cain, 1952). We agree with most other workers that the rare species have little to do with community organization, being insignificant numerically, whereas the relatively few ubiquitous species give the community its characterization and are essentially responsible for its biological activity.

LITERATURE CITED

The literature on soil microarthropods is much more extensive than the cited papers would indicate. Because our results are in general agreement with those of most other authors and because we have made different uses of the data, only a few of the many excellent papers on the subject have been listed. The reader interested in obtaining a more complete bibliography is referred to the papers by Macfadyen (1952) and especially Fenton (1947).

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK, and K. P. SCHMIDT.

1949 Principles of animal ecology. Philadelphia and London: W. B. Saunders Co.

ANSCOMBE, F. J.

1949 The statistical analysis of insect counts based on the negative binomial distribution. Biometrics, 5: 165-73.

BRIAN, M. V.

1953 Species frequencies in random samples from animal populations. Journ. Animal Ecol., 22: 57-64.

CAIN, S. A., and F. C. EVANS

1952 The distribution patterns of three plant species in an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 52: 1-11.

DICE, L. R.

1952 Natural communities. Ann Arbor: Univ. Mich. Press. Pp. i-x + 547, 52 figs.

DOWDY, W. W.

1944 The influence of temperature on vertical migration of invertebrates inhabiting different soil types. Ecology, 25: 449-60.

EVANS, F. C.

1952 The influence of size of quadrat on the distributional patterns of plant populations. Contrib. Lab. Vert. Biol. Univ. Mich., 54: 1-15.

EVANS, F. C., and S. A. CAIN

1952 Preliminary studies of the vegetation of an old-field community in southeastern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., 51: 1-17, 2 pls.

FENTON, G. R.

1947 Essay review. The soil fauna: with special reference to the ecosystem of forest soils. Journ. Animal Ecol., 16: 76-93.

FISHER, R. A., A. S. CORBET, and C. B. WILLIAMS

1943 The relation between the number of species and the number of individuals in a random sample of an animal population. Journ. Animal Ecol., 12: 42-58.

HOFFMANN, C. H., H. K. TOWNES, H. H. SWIFT, and R. I. SAILER

1949 Field studies on the effectiveness of airplane applications of DDT on forest invertebrates. Ecol. Monogr., 19: 1-46.

MACFADYEN, A.

1952 The small arthropods of a Molinia fen at Cothill. Journ. Animal Ecol., 21: 87-117.

MYERS, E., and V. J. CHAPMAN

1953 Statistical analysis applied to a vegetation type in New Zealand. Ecology, 34: 175-85.

PEARSE, A. S.

1946 Observations on the microfauna of the Duke Forest. Ecol. Monogr., 16: 127-50.

PRESTON, F. W.

1948 The commonness, and rarity, of species. Ecology, 29: 254-83.

SALT, G.

1952 The arthropod population of the soil in some East African pastures. Bull. Entomol. Res., 43: 203-20.

SALT, G., F. S. J. HOLLICK, F. RAW, and M. V. BRIAN

1948 The arthropod population of pasture soil. Journ. Animal Ecol., 17: 139-50.

SCHMIDT, K. P.

1946 The new systematics, the new anatomy, and the new natural history. Copeia, 1946, pp. 57-63.

STRENZKE, K.

1951 Die Biozönotik der Oribatiden norddeutscher Böden. Naturwissenschaften, 38: 284-85.

STRICKLAND, A. H.

1947 The soil fauna of two contrasted plots of land in Trinidad, British West Indies. Journ. Animal Ecol., 16: 1-10.

SVERDRUP, H. U., M. W. JOHNSON, and R. H. FLEMING

1946 The oceans; their physics, chemistry and general biology. New York: Prentice-Hall.

WILLIAMS, C. B.

1953 The relative abundance of different species in a wild animal population. Journ. Animal Ecol., 22: 14-31.

WILLIAMS, E. C.

1941 An ecological study of the floor fauna of the Panama rain forest. Bull. Chicago Acad. Sci., 6: 63-124.

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price, $0.75.

CONTRIBUTIONS FROM THE LABORATORY OF VERTEBRATE BIOLOGY

University of Michigan, Ann Arbor, Michigan

Number 65 March, 1954

A DESCRIPTION OF A SUBHUMID CORRIDOR ACROSS NORTHERN CENTRAL AMERICA, WITH COMMENTS ON ITS HERPETOFAUNAL INDICATORS

By L. C. STUART

Accepted for publication June 1, 1953

CONTENTS

Introduction 1
Sources of Data 4
Description of the Corridor 5
Herpetofaunal Indicators of the Corridor 12
Discussion 21
Summary 24
Literature Cited 25

INTRODUCTION

IT IS well known that deserts, or at least subhumid climatic conditions, along the east coasts of land masses within the limits of the tropics are extremely rare. Theoretically, in fact, subhumid climates cannot possibly occur in such locales. Yet where rain-shadow conditions exist or where local air movements produce abnormal conditions, dry-lands do occur in certain tropic east-coast areas. Two such regions in northern Central America have long been known to biologists, the Comayagua Valley of Honduras and the valley of the middle and upper Río Motagua in Guatemala (see Map 1 for the locations hereinafter mentioned).

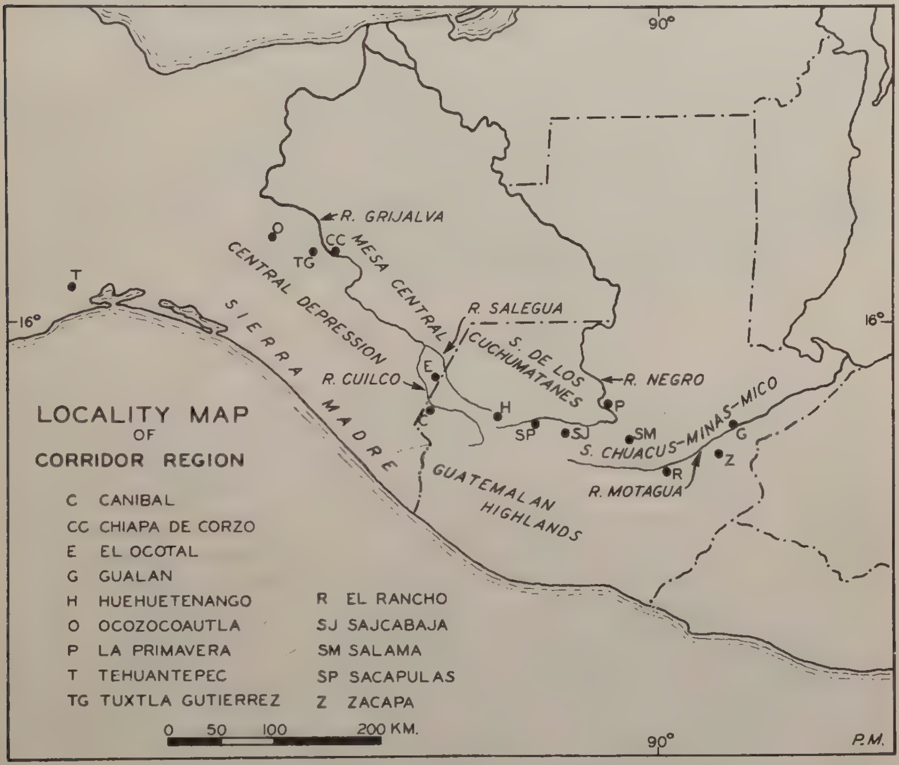
For some years I have been accumulating data on the fauna of the latter region as well as on that of the adjacent dry-lands of central Guatemala, and, as a result, some rather interesting geographic anomalies have been uncovered. As yet no faunal data on the Comayagua Valley have been forthcoming.

Of particular interest is the fact that certain groups of reptiles and amphibians are rather extensively distributed over the drier parts of central and southeastern Guatemala and along the none-too-mesic Pacific versant of eastern Guatemala and El Salvador and in some cases as far south as Costa Rica. The immediate systematic affinities of these groups are found in southern Mexico despite the fact that there is no geographic continuity in the Mexican and Central American populations along the lowlands of either the Pacific or Caribbean,where continuity would normally be sought. In order to explain this perplexing situation I was led to examine the distribution and the faunas of the various dry-land environments of northern Central America and southern Mexico.

As a result of investigations carried on particularly in 1952 and 1953, it was discovered that a chain of dry-land environments extends from the Isthmus of Tehuantepec (Pl. I, Fig. 1) to the xeric Motagua Valley of Guatemala, from which there are ample subhumid pathways (Pl. I, Fig. 2) for dispersal both eastward into Honduras and southward to lower Central America. The crux to the solution of the whole problem, however, is the corridor that connects the Isthmus of Tehuantepec with the middle Motagua Valley. It is the purpose of this paper to call to the attention of biologists this dry-land corridor that crosses northern Central America. As yet information is very incomplete, and the evidence herein presented is at best scanty, but it is hoped that a presentation of my own findings at this time may prove of some service to investigators working with the distributions of groups other than the amphibians and reptiles.

This corridor cuts through the highlands of Chiapas and Guatemala and, with the exception of narrow breaks, lies for the most part below elevations of 1000 m. The environment throughout the length of the corridor is essentially subhumid and, though broken at higher elevations by oak and pine forests, supports a cover of dry-forest, grassland, and desert vegetation types. Though various biologists have at several times recognized the distinctness of the environment at either end of the corridor, none has ever given consideration to the possibility of its continuity across the Central American isthmus. Smith (1939) placed the Grijalva (Mexican) section in his Chiapan Plateau Biotic Province. Goldman and Moore (1945) considered this section to be a part of their Tehuantepec Biotic Province, which included in addition to the Grijalva Valley and the Isthmus of Tehuantepec dry-lands the Pacific coastal plain of Chiapas and Guatemala. Goldman (1951) did not modify this scheme. Smith (1949) included the Mexican section in his Palenque Province,which he considered as a part of the Atlantic Subregion,and thus inferred closer relationship to the mesic Caribbean versant than to the drier Pacific side. At the other end of the corridor in Guatemala Stuart (1943) recognized the distinctness of the dry-lands of Guatemala in referring them to his Zacapan Biotic Province, and Smith (1949) followed this same scheme. Neither of these two works, however, recognized any relationship between the Mexican and Guatemalan sections. This paper will not give consideration to the faunal position of the different parts of the corridor, but will be limited to a description and a discussion of the biological significance of the region.

Though I had visited such parts of the corridor as the Salamá Basin (Schmidt and Stuart, 1941) and the lower Río Negro and Motagua sections as early as 1938, it was not until 1947 that I became concerned with the Mexican section as a result of a visit to the Cuilco Valley in the headwaters of the Río Grijalva. Finally, in 1952 and 1953 I was able to visit and study the entire Mexican part of the corridor from Tehuantepec through the Central Depression of Chiapas, and in the former year I was also able to investigate in some detail the Motagua division. It was these last investigations that crystallized the ideas which are presented herein.



Map 1

The maps of the distributions of the several species of lizards have been compiled from a number of sources. I have included, therefore, only the localities of which I am reasonably certain, and the majority of those through the corridor have been checked personally. In the case of *Enyaliosaurus, clarki* occurring in Guerrero could not be shown. In other instances only pertinent records are shown in extralimital regions.

Acknowledgments

In gathering data for this paper I have had the close co-operation of many individuals and institutions. For the privilege of examining collections in their charge (some of them unstudied) I am indebted to Mr. Charles E. Bogert of the American Museum of Natural History, Mr. Clifford Pope of the Chicago Natural History Museum, Dr. Edward H. Taylor of the University of Kansas, and Dr. Doris Cochran of the United States National Museum. I am particularly indebted to my colleagues at the University of Michigan, Dr. Norman E. Hartweg and Dr. Charles M. Walker. In addition to permitting me access to the herpetological collections of the Museum of Zoology, they have constantly aided me in the solution of problems that have arisen in regard to systematic and geographic matters. I have also been fortunate enough to have discussed a number of problems with Dr. Claude Hibbard of the Museum of Paleontology, University of Michigan. Financial support for field investigations has been supplied at various times by the Baird Exploration Fund, the Faculty Research Fund, and the Horace H. Rackham School of Graduate Studies, all of the University of Michigan. To all of these I wish to express my sincere thanks.

SOURCES OF DATA

Aside from the technical sources on the geology, climatology, and vegetation of the region under discussion, all of which are given in the Literature Cited, I have had access to collections of reptiles and amphibians secured through my own efforts or through those of my colleagues. In addition to studying these collections I have made extensive notes on various features of this dry-land corridor which throughout most of its extent I have visited personally. A summation of the sources from which these collections have been secured and from which the notes have been drawn seems to be in order.

Isthmus of Tehuantepec and environs. — The only comprehensive account of the herpetology of the isthmian region proper is that of Hartweg and Oliver (1940). Though I have not collected in the region, I spent several days in the environs of Tehuantepec and crossed the Isthmus to the wet forest on the Gulf of Mexico side. I have also crossed the Inter-American Highway which traverses the entire length of the Tehuantepec plains before climbing over the Sierra Madre into the Grijalva Valley. This last trip I have made on four different occasions.

Middle Grijalva Valley. — Smith (1946) has supplied some knowledge of the herpetofauna in the region of Ocozocoautla. I have also had access to material collected by my colleague, Norman E. Hartweg, who spent some days in the vicinity of Chiapa de Corzo. I have passed through the region on several occasions.

Upper Grijalva Valley. — I have studied this region briefly in both Mexico and Guatemala. In 1947, while studying the southwestern highlands of Guatemala, I crossed the Sierra Madre and descended into the valley of the Río Cuilco at Canibal close to the Mexican border, where I spent several days collecting. In 1953 I spent four days collecting in the region of El Ocotal (Ciudad Cuauhtémoc) near the Guatemalan border. Here most of my collecting was done along the Río San Gregório and on the flats drained by small tributaries of that river which joins with the Cuilco and lesser streams to form the Grijalva.

Río Negro Valley. — Although I have spent several days in Sacapulas, I have never done any extensive collecting in the region. From farther downstream, north of Cubulco, the British Museum (Natural History) has some material which was collected during the latter half of the nineteenth century. Below that point at Chixoy, near La Primavera, I spent several days collecting in 1940. Of the higher basins that are drained by tributaries of the Río Negro only that of Salamá is known (Schmidt and Stuart, 1941). I passed through all of these basins, however, when I made a foot journey from Salamá to Sacapulas in 1944.

Río Motagua Valley. — During the course of carrying on investigations on the southeastern uplands of Guatemala in 1952, I spent some three weeks in the El Rancho region, both at the village itself and at Finca Los Leones in a tributary valley to the northwest of El Rancho. Slevin (1939, 1942) has reported on material which he collected at Progreso, a village in a tributary valley of the Motagua, only a few kilometers southwest of El Rancho. I have also had access to material collected by Mr. Townsend Sackett in the Zacapa region. A few miscellaneous specimens from Gualán are preserved in the collections of the United States National Museum.

DESCRIPTION OF THE CORRIDOR

Geology. — Inasmuch as the corridor is made up of three separate valley systems with intervening mountain ranges and in places small basins drained by tributaries of the main streams, a geological summation is difficult. It is necessary, therefore, to treat each major valley as an entity. Needless to say, the summary works of Schuchert (1935) and Sapper (1937) are the authorities on which the following description is based.

The corridor begins in the north with the valley of the Río Grijalva. This valley, more generally known as the Central Depression of Chiapas, is oriented roughly in a northwest-southeast direction. To the southwest it is bounded by the Sierra Madre which, beginning as a low range at the Isthmus of Tehuantepec (long. 94°), increases in height toward the southeast and terminates in southwestern Guatemala (long. 92°). On the northeast side of the depression the Mesa Central rises in a sharp escarpment. Though several geologically distinct blocks are involved, this Mesa Central presents an upland area that is more or less continuous with the Sierra de los Cuchumatanes of southwestern Guatemala. Between these two highland masses the Central Depression lies as a graben whose northwestern entrance opens into the Isthmus of Tehuantepec and whose southeastern end abuts the Sierra de los Cuchumatanes. The valley has a length of about 175 km. and a maximum width of possibly 50 km.

Cretaceous limestones outcrop more or less continuously throughout the length of the valley, and these beds are apparently of the same formations that occur in southwestern and central Guatemala. Though the Sierra Madre is composed of ancient sedimentary and igneous rocks, some of which are apparently of Permian age, the Mesa Central is composed entirely of young sedimentaries, some as recent as Miocene. The graben-horst structure of the Central Depression and its bordering highlands was unquestionably the result of the Pliocene orogeny which was responsible for most of the extant configuration of northern Central America.

Throughout its course in the graben the fall of the Río Grijalva is slight. Its flood plain in the neighborhood of the Guatemalan border lies at an elevation of about 700 m., and at the lower end of the valley at Chiapa de Corzo it has an elevation of about 400 m. The floor of the depression, however, is by no means level. Tributaries of the Grijalva, especially from the south, have dissected the valley slopes and floor to produce terrain of moderate to high relief in various places. At no locality within the graben are elevations in excess of 1200 m. encountered.

At the upper (Guatemalan) end of the valley the Río Grijalva takes on a frayed appearance as its tributaries from the Sierra de los Cuchumatanes and from the Sierra Madre converge to form the main stream. The graben structure of the valley, too, comes to an end, and canyon-like tributary valleys slash back into the mountains. Some of these valleys appear to follow structural lines, whereas others appear to be entirely erosional in their origins. My interest lies in only two of these valleys, that of the Río Saleguá, whose lower course in Mexico is known as the San Gregório, and that of the Río Cuilco.

Throughout its course in Guatemala the Saleguá flows through a narrow V-shaped valley that lies between the southern edge of the Sierra de los Cuchumatanes and a local highland block known as the Sierra de Cuilco. The valley, which is a linear projection of the Central Depression of Chiapas, is probably structural. The gradient of the stream through this part of its course is considerable, its fall amounting to no less than 1000 m. between its source in the Huehuetenango region and the Mexican border, a distance of about 65 air-line kilometers.

The Cuilco through most of its course similarly occupies a deep V-shaped valley (Pl. III, Fig. 1). Arising on the crest of the Sierra Madre in Guatemala, the stream flows eastward, loops around the eastern and northern sides of the Sierra Madre, and continues northwestward to join the San Gregório in the eastern end of the Central Depression. The gradient of the Cuilco, like that of the Saleguá, is considerable, and at least part of its course, where it passes between the Sierra Madre and the Sierra de Cuilco, is canyon-like. At the eastern end of the Sierra de Cuilco, the Saleguá and Cuilco are separated by only a narrow, low ridge. The valley of the Cuilco is probably erosional rather than structural.

The Grijalva drainage comes to an end on the rolling uplands in the vicinity of Huehuetenango, where the continental divide attains an elevation of roughly 1900 m. (Pl. IV, Fig. 1). To the east of the divide are encountered the headwaters of the Río Negro. Though the source of this stream is generally taken as a large spring in the vicinity of Aguacatán, most of the waters of the upper river are derived from the plateau lands to the south.

Intrenched in a narrow valley from its very source, the Negro plunges into a gorge at the level of Sacapulas and continues to flow in a deep canyon due eastward for a matter of some 60 km. In a great S-shaped flexure it then breaches the highlands of El Quiché and Alta Verapaz (Pl. IV, Fig. 2) and flows out onto the lowlands of the Yucatán Peninsula toward the north. The origin of this upper valley of the Río Negro is obscure, and it is evident that the history of drainage lines through this region has been extremely complex. Nevertheless, it seems fairly certain that the extant gorge of the Negro is structural and dates from the Pliocene. It lies just to the south of a great fault that separates the younger limestone mountains (the Cuchumatanes and the Sierra de Uspantán) on the north from the ancient and extremely complex mass (Sierra de Chuacús) to the south. Like the headwaters of the Grijalva, the Negro in its upper course has a steep gradient, falling between its source and the confluence of the Río Salamá some 900 m. in a 90 km. air-line distance.

Most of the tributaries of the upper river enter from the south, and these have carved basins of considerable size into the northern flanks of the Sierra de Chuacús. Of these, the basins of Sajcabajá, Rabinal-Cubulco, and Salamá (Pl. V, Fig. 1) are the largest. These basins decrease in elevation from west to east, that of Sajcabajá lying at 1250 m., whereas that of Salamá does not exceed 950 m. Bordering these basins on the south is the main crest of the Sierra de Chuacús and Sierra de las Minas, which presents a formidable barrier between the drainages of the Negro to the north and of the Motagua to the south. There are, however, a number of low passes, less than 1500 m. in elevation, through this range. These open into short, steep valleys that plunge down into the Río Motagua. In fact, between Rabinal and Salamá the Chuacús range is considerably lower than to either the east or west, where elevations of 2500 m. are attained.

Paralleling the Río Negro to the south and separated from it by the Sierra de Chuacús, which continues eastward to the Caribbean as the Sierra de las Minas and the Sierra de Mico, is the valley of the Río Motagua. Rising on the Guatemalan Plateau in the vicinity of Santa Cruz Quiché, the Motagua flows eastward to the Caribbean, some 300 km. away. This valley is, in the main, structural in origin. It lies between two ancient masses, the Chuacús-Minas-Mico range to the north and a badly eroded, unnamed ridge (Pl. I, Fig. 2, and Pl. VI, Fig. 1) to the south. Both of these masses were further uplifted during the Pliocene, an event which also rejuvenated the upper course of the Motagua.

The upper third of the valley is of steep gradient and narrow, as may be judged by the fact that in the first 120 km. of its course the river falls from 2000 m. at its source to 300 m. at El Rancho. Below this latter point the valley widens, and at Zacapa, 55 km. east of El Rancho, at the confluence of the Río Zacapa, the flood-plain is roughly 20 km. broad. From El Rancho eastward the local relief of the valley decreases, and in the vicinity of Zacapa the river is intrenched in a broad plain. For the most part, this middle section of the valley is covered with a deep mantle of alluvial materials which have been deposited by the main stream in times of flood and by the numerous tributaries which enter the river from the south.

Below Zacapa the river cuts through a local ridge, and the valley narrows. But below Gualán the valley again broadens, and the lower third of the Motagua meanders through a lowland area that is dotted with oxbows and swamps and is extensively inundated during the wet season. My interest lies in the central part of the Motagua Valley between Gualán and El Rancho.

Throughout the entire length of the corridor uplift is still an active process, as is evidenced by the terrace systems along the stream courses (Pl. III, Fig. 1, and Pl. VI, Fig. 1). In many places these terraces are well defined,and except in gorge areas the streams are everywhere well intrenched in ancient flood-plains.

In summarizing the geology of the corridor three points may be made. First, the corridor consists of a series of valleys and basins that have apparently existed since the late Miocene or early Pliocene in a region in which uplift is continuing. Second, though much of the corridor lies below the 1000 m. contour, an important biotic isopleth in northern Central America, elevations of as much as almost 2000 m. separate the three major drainages that are included in the corridor. Third, except for the middle valleys of the Rios Grijalva and Motagua, the corridor at no place presents an extensive dry-land environment. It is, in fact, often restricted to gorges that may be no more than a few hundred yards in width (Pl. III, Fig. 1 and Pl. IV, Fig. 2).

Climate. — Throughout most of its course the corridor may be described as hot and subhumid. Aside from reports from a mere handful of stations, however, there are no very definite data on the climate of the region, and what little is known has been summarized by Ward and Brooks (1936) and by Sapper (1932).

For the most part, the temperature of the corridor lies within the *A* (frost free) boundary of Köppen (1923). With a latitudinal extent of but 2°, and all of it essentially dry, temperature variations within the region are largely a function of altitude. It is indicated that there is an altitudinal decrease in temperatures amounting to about 0.6° (all temperatures herein are given in degrees centigrade) per 100 m. for mean annual temperatures and possibly somewhat less for the mean temperature of the coldest month. As a generalization, therefore, the *A-C* boundary probably lies somewhere in the neighborhood of the 1000 m. contour. Thus, only in the headwater regions of the Grijalva and Negro drainages and through the passes over the mountains that separate the basins of central Guatemala from the valley of the Río Motagua are other than tropical temperatures encountered. In the Mexican section of the corridor the mean annual temperature of Tuxtla Gutiérrez (550 m.) is 24.4° and of Motozintla (1310 m.), 18.9°. Typical stations in Guatemala, Zacapa (180 m.) and Salamá (920 m.), have mean annual temperatures of 26.4° and 22.6°, respectively. The mean temperatures for the coldest month (December or January) for these same four stations are 21.2°, 16.0°, 23.5°, and 19.9°, respectively. The range in temperature between the coldest and warmest months is in the neighborhood of 6°.

Though much of the region falls within the humid boundary of Köppen, it may be pointed out that even these areas lie very close to the *B* boundary and that high relief in many sections and porous soils in others greatly reduce the effectiveness of the rainfall. Sources from which the precipitation of the corridor stems are not of present interest, and it is sufficient to point out that throughout its entire extent the corridor lies within the rain-shadow of the high mountains and plateaus which border it to the north and northeast. The most humid part of the corridor is probably the lower Grijalva Valley, which at Tuxtla Gutiérrez receives almost 900 mm. of rainfall annually. Farther up the valley, at Motozintla, the annual precipitation amounts to no more than 650 mm. The driest known section of the corridor is the middle Motagua Valley where annual rainfall does not exceed 600 mm., but it is not improbable that parts of the gorge of the Río Negro and headwater valleys of the Grijalva in Guatemala receive even less moisture. Throughout the corridor approximately 90 per cent of the precipitation is deposited during the high-sun period.

Thus, though the Grijalva Valley through its middle course lies within the *Aw* climatic type of Köppen below 1000 m. and probably *Cw* above that level, it is all very close to the *B* boundary. The same may be said of the upland basins of central Guatemala. All of the middle valley of the Río Motagua may be classified as *BS*, and it is not improbable that when data are available, the upper courses of the Grijalva and the Negro will prove to be *BW*.

Vegetation. — Among the various authors who have described or mapped the vegetation of regions through which the corridor passes there seems to be little agreement. From personal experience I am inclined to accept the work of Miranda (1952) on the Grijalva section and those of Steyermark (1950) and Sapper (1894) on the Guatemalan section as the most reliable.

Miranda mapped the floor of the Central Depression of Chiapas as basically savanna throughout its length. This does not imply that the valley consists of an unbroken grassland. Indeed, much of the valley supports stands of low dry forest, patches of mesquite-like thickets, occasional stands of palms, and, along the water courses, gallery forest. Where savanna does occur, the grassy plains are dotted with stunted trees, which may occur singly or in small groves (Pl. II, Fig. 1). In the upper parts of the valley a cover of low shrubs and small trees, largely acacias, is not uncommon (Pl. II, Fig. 2). These may form impenetrable thickets or, more often, may be scattered over the grasslands to produce a more open brushland. The forests of low, deciduous trees, rarely over 10 m. in height, are especially common in the upper end of the depression. These forest groves, though appearing to be dense jungle from without, are, in reality, fairly open with little undergrowth and with a deep mantle of dry leaves on the forest floor. Palm groves are extremely local. Along the major water courses a narrow strip of gallery forest may generally be found. Inasmuch as the majority of the streams are deeply intrenched, this type of forest is restricted to the steep river banks and breaks off sharply at the edge of the higher land.

The main slopes of the depression and higher ridges within the valley support, in the main, dry forests and brushland. At higher levels (above about 1000 m.) oak makes its appearance, and pine is not uncommon on the crests of the ridges.

Generally speaking, the greater part of the valley is devoted to the grazing industry. Clearing of the land and firing have destroyed considerable virgin cover, and planted pasturage not infrequently obscures the virgin condition. But taken as a unit, the vegetation of the Central Depression all points toward subhumid conditions.

The headwater valleys of the Grijalva system support a vegetation cover that is almost desert in aspect. At Canibal the valley floor was without a continuous sod cover (Pl. III, Fig. 1). Dense thickets of mesquite and other xeric shrubs and an abundance of *Cereus*-like cacti and prickly pears form a cover that is known as *espinal* (Pl. III, Fig. 2). Even gallery forest was lacking along the water courses. The steep valley slopes support a rank growth of desert shrubs and stunted trees (Pl. III, Fig. 2) which, above the 1300 m. contour, shades into pine and oak.

The highlands in the vicinity of Huehuetenango which form the divide between the Grijalva and Negro drainages lie within the oak-pine belt (Pl. IV, Fig. 1). For the most part, the forests of this region are open, with little underbrush, and lack continuity. Possibly owing to long occupation by Indians and Europeans who may have cleared much of the forest land, there are, in the region, extensive stretches of steppe grasslands.

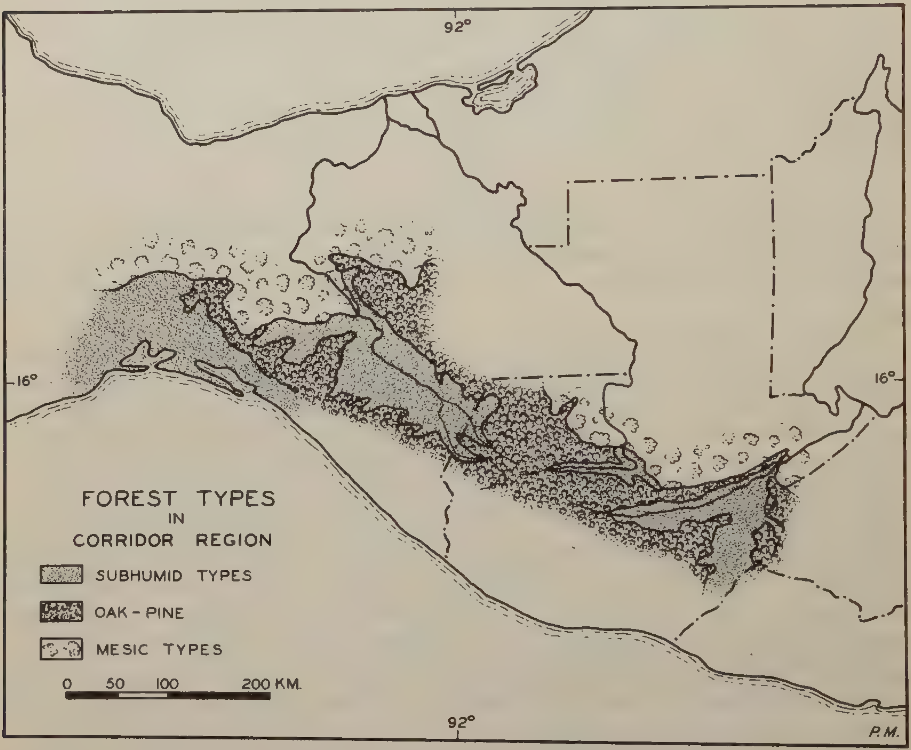
Upon entering the valley of the Río Negro at Sacapulas one encounters a vegetation cover that is in most respects similar to that of the Cuilco region. I am unfamiliar with the gorge down to the entrance of the Río Salamá, but Sapper mapped it as grass and shrub steppe with chaparral and *Cereus*-form cacti. In the region of Chixoy, well below the entrance of the Salamá, the character of the vegetation is somewhat more mesic (Pl. IV, Fig. 2), but there is little reason to suspect that any more humid types occur between Sacapulas and the point at which the Negro enters the lowlands of the Yucatán Peninsula. Throughout this region the oak-pine belt on the upper valley slopes extends somewhat farther down than at Canibal. At La Primavera, for instance, one encounters open oak and pine forests at about the 1000 m. level.

Depending upon elevation, the basins that drain northward into the Río Negro support varied types of cover. The highest and most westerly, that of Sacabajá, may be classified as a pine-savanna. For the most part, a cover of tall savanna grasses features the basin, and the pine occurs in open groves. Along the water courses a narrow band of open broadleaf forest may be present. The Rabinal-Cubulco Basin, the middle of the three major basins, is much like that of Sacabajá in the west, but in the east a cover of short grasses and dry-land shrubs takes over. The most easterly and the lowest, the Salamá Basin, is steppe land with low, dry-land shrubs and many varieties of small cacti (Pl. V, Fig. 1). As it is relatively intensively cultivated, there is difficulty in judging just what primeval conditions were. In all instances the mountain slopes above the basins support a cover of pine and oak at elevations up to about 1500 m. (Pl. V, Fig. 2), where the cloud forest begins.

Between the basins of central Guatemala and the Motagua Valley the massive Sierra de Chuacús supports on its north side a cloud forest above the 1500 m. contour, but on its south (lee) slopes this wet forest type is not encountered lower than about 2000 m. Below those levels oak and pine form the dominant cover. The latter forests are fairly open but provide a somewhat mesic environment. In the region under discussion the mountains, as previously noted, break down somewhat, and much of the crest to the south of the basins lies below the cloud-forest level. On the south slopes of the range oak and pine predominate down to about the 1000 m. level, below which desert shrubs form a dense tangle. The desert landscape of the Motagua Valley is not encountered until one descends to roughly the 500 m. level.

The vegetation of the middle Motagua Valley has been classified as "desert-chaparral" by Steyermark, a term that he applied also to vegetation of the Río Negro gorge. Perhaps the most striking feature of the cover is the abundance of the large, *Cereus*-like cacti (Pl. VI, Fig. 2). Depending upon relief, water table, and other physical features, there is considerable variation in the cover of this part of the valley. Rocky knolls support rank growths of spiny desert shrubs and cacti; more level plains may resemble short-grass steppe lands with scattered low trees of the acacia type or extensive thickets of mesquite (Pl. VI, Fig. 2); intermittent stream courses are lined with stunted deciduous trees, shrubs, and dense stands of cacti; whereas along permanent water courses a narrow band of gallery forest may prevail. Toward the west, as the uplands of the plateau are approached, the desert landscape gives way to dry brushland and oak forests, and to the east toward the Caribbean lowlands, where conditions become more mesic, the desert landscape shades gradually into the wet forest of the lower valley. Gualán appears to serve as a suitable boundary limiting the eastward extent of the desert.

Thus, throughout the entire extent of the corridor from the Isthmus of Tehuantepec to the Motagua Desert an essentially xeric type of cover prevails. Even where forests do occur, with the exception of the gallery forests that may border larger streams, they are of types which are characteristic of subhumid lands. Map 2 shows the distribution of the major vegetation formations in the corridor region.



Map 2

HERPETOFAUNAL INDICATORS OF THE CORRIDOR

It is not within the bounds of this paper to discuss the herpetofauna of the dry-land corridor in its entirety. Indeed, no part of the corridor is known in sufficient detail to permit such a discussion. Smith (1946) has commented briefly on a collection of reptiles and amphibians from the middle Grijalva Valley, and Schmidt and Stuart (1941) have given a short account of the herpetofauna of the Salamá Basin. Other than the data in these two works, our present knowledge of the fauna of the corridor is drawn from scattered collections from miscellaneous stations which have yielded only the commoner species of the various areas.

A study of these collections reveals the fact that there is little unity in the herpetofauna of the corridor as a whole. The fauna of any one station does, it is true, contain certain forms which seem to be generally distributed throughout the dry-lands of northern Central America and southern Mexico, but the fauna of any single station is often characterized by the presence of species that are more frequently components of adjacent biotic areas than of the corridor itself. Thus, were one to compare the list of species known from the middle valley of the Río Motagua with the list presented by Smith for the middle Grijalva Valley, one would find little in common in the two areas. Furthermore, the rarities upon which faunal similarities and dissimilarities are so often based have not as yet been secured in the haphazard collecting that has characterized field investigations in the corridor.

Any suggestion of continuity in the fauna of the corridor must stem, therefore, from certain species that occur abundantly in their respective habitats and which are not apt to be overlooked by even the most casual collector. It is, in fact, through an analysis of certain forms of high productivity that the biological importance of the corridor is best illustrated. Some of the forms, therefore, that I consider sufficiently well known to serve as "indicators" will be briefly examined.

Hypopachus championi Stuart

Described from the Salamá Basin, this species has since been found to be widely distributed over the southeastern uplands of Guatemala. Insofar as is known, its vertical limits are relatively narrow. To date it has not been secured at elevations below 900 m. nor above 1500 m. Indeed, over most of Guatemala it is replaced by some member of the *inguinalis* group above the latter elevation. It appears, therefore, to be confined to the upper parts of the savanna and desert-shrub environment and to the lower parts of the oak or oak-pine zone.

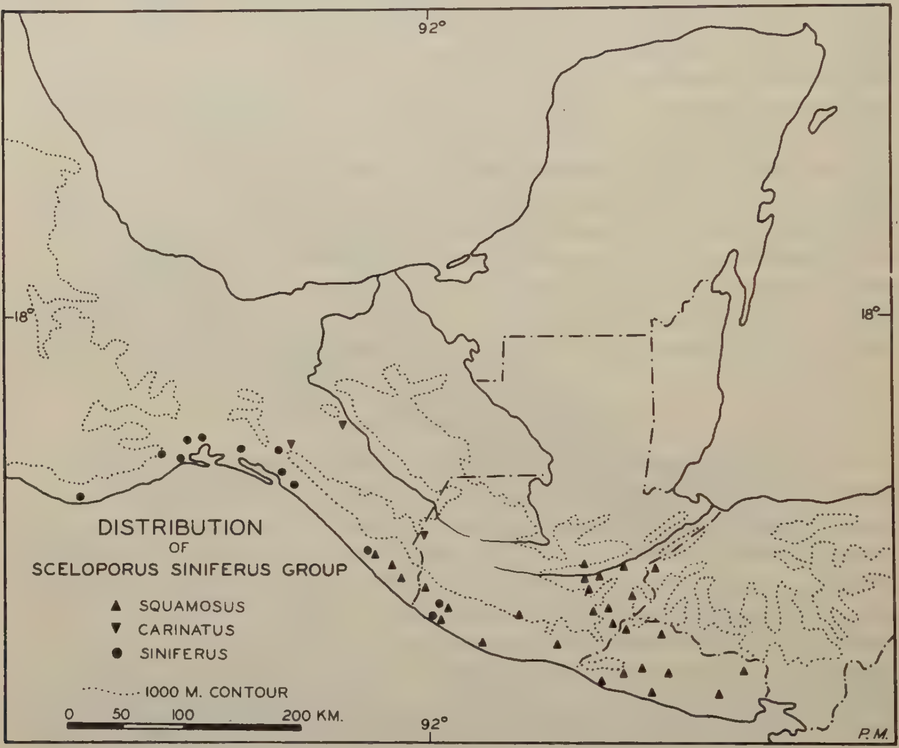
Though a member of a lowland group, it is not a subspecies of *cuneus*, which is widely distributed over the lowlands of the Caribbean versant of northern Central America and Mexico and also appears in the United States. It is most closely related, rather, to *Hypopachus maculatus* Taylor, which is known only from the middle Grijalva Valley. The genus is unknown from the Pacific versant south of the Isthmus of Tehuantepec.

These two closely related forms, *H. championi* and *H. maculatus*, though now lying at either end of the corridor and failing to contact each other geographically, strongly suggest previous continuity.

Sceloporus, siniferus group
(Map 3)

This small group of scelopori is distributed from Guerrero southward to Nicaragua. With the exception of a small population of *squamosus* in central Guatemala and in northern Honduras, the group is essentially one that is distributed along the Pacific versant of southern Mexico and Central America.

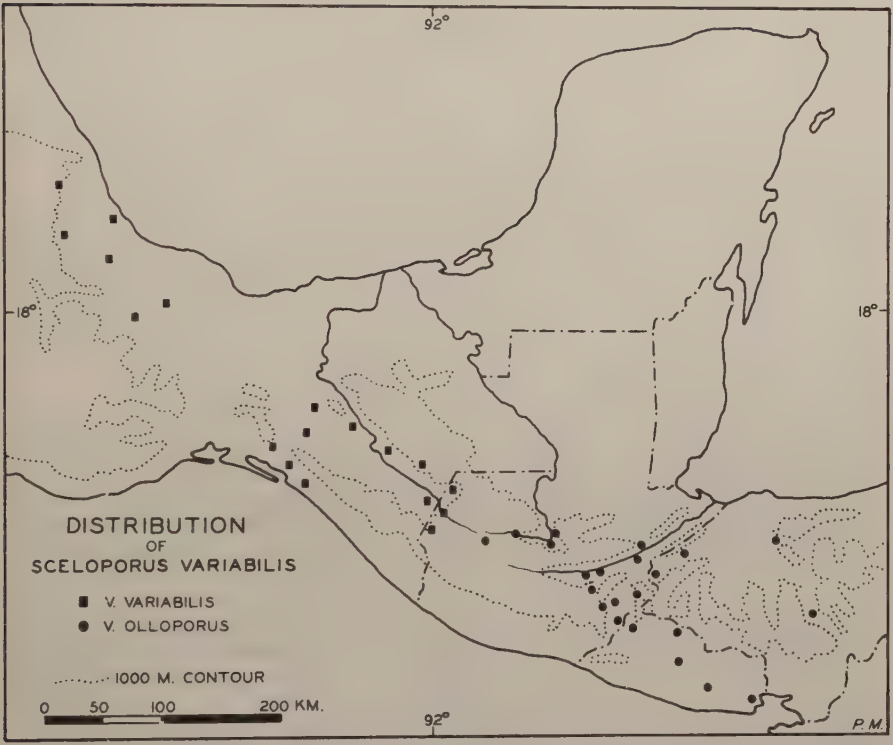
Smith (1939: 300-302), though admitting close affinity between *squamosus* and *carinatus*, gave a somewhat ambiguous presentation of the specific interrelationships of the group. Excluding *ochoterenae*, which is but remotely related to other members of the group, the remaining four species appear to be contained in two subgroups, i. e., *siniferus* and *cupreus*, as opposed to *carinatus* and *squamosus*. The former two are distributed along the Pacific versant from Guerrero to western Guatemala. The latter two extend from the western end of the Grijalva Valley through the dry-land corridor to the Motagua Valley and thence southward across the southeastern uplands of Guatemala to the Pacific versant along which *squamosus* is distributed from eastern Chiapas to Nicaragua.



Map 3

On the basis of available data it would appear that from a prototypic population a "*siniferus*" division split off in one direction and a "*carinatus*" division in another. From the former developed the modern *siniferus* and *cupreus*, and from the latter *carinatus* and *squamosus*. This final stage in the evolution of the modern forms probably took place *in situ*. At any rate, the overlap in the ranges of *siniferus* and *squamosus* in western Guatemala and eastern Chiapas suggests fairly remote relationships between the two.

Thus, in the absence of extent continuity, through their obvious phylogenetic relationship suggesting previous geographic continuity, *S. carinatus* and *S. squamosus* parallel the situation observed in *H. championi* and *H. maculatus*.



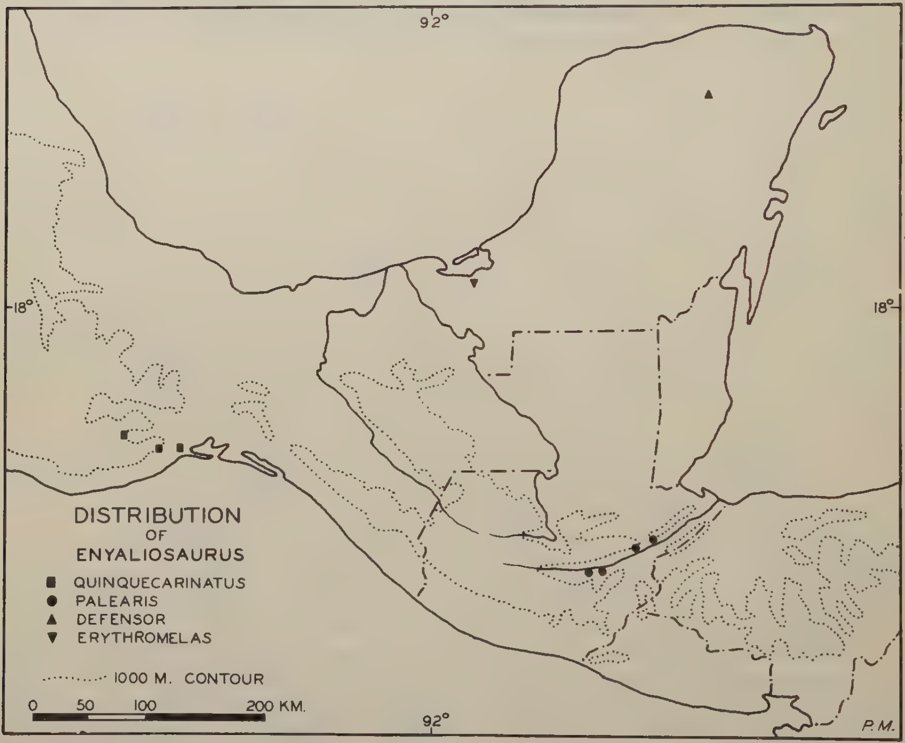
Map 4

Sceloporus variabilis subspp.
(Map 4)

This species ranging from Texas to Costa Rica includes about a half-dozen subspecies of which only two, *variabilis variabilis* and *variabilis olloporus*, are factors in the problem at hand. The typical form extends from southern Tamaulipas southward along the coastal plain of the Gulf of Mexico and the eastern side of the Mexican Plateau across the Tehuantepec isthmian region and into the Grijalva (Cuilco) Valley in southwestern Guatemala. It is known from sea level to at least 1900 m. elevation. In southwestern Guatemala (Canibal) it appears to intergrade with *olloporus*.

This latter form occurs through the dry-lands of central Guatemala southward to Costa Rica. It has been taken from near sea level to an elevation of 2200 m. South of southeastern Guatemala and north-central Honduras it appears to be restricted to the Pacific versant.

It is important to note that no form of the subspecies is known from the Pacific versant from the Isthmus of Tehuantepec at least as far south as El Salvador. The *variabilis* group is represented on the Caribbean versant from southern Veracruz to Honduras (i. e., the lowlands of the Yucatán Peninsula) by two species, *cozumelae* and *teapensis*, neither of which is particularly closely related to either *variabilis* or *olloporus* even though placed by Smith (1939) in the same group.

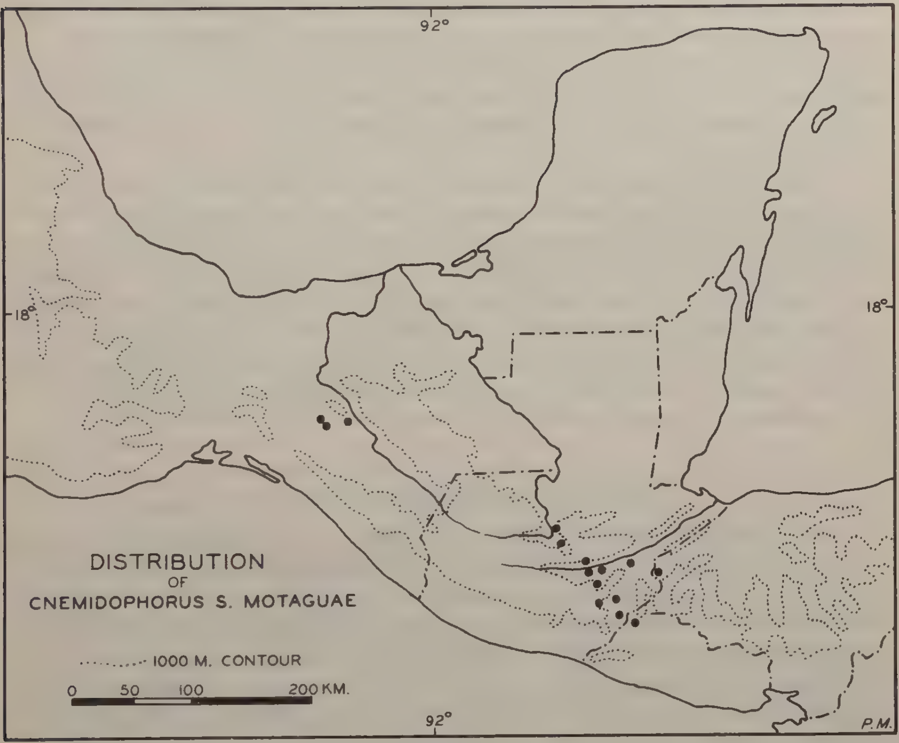


Map 5

Such gaps in the distribution of these two forms as appear on the map are indicative only of insufficient collecting. In attaining elevations of 2200 m. it is evident that the two find no barriers throughout the length of the corridor. Their geographic continuity is the most complete of any form found in the corridor.

Enyaliosaurus spp.
(Map 5)

All geographic data suggest that *Enyaliosaurus* is a relict genus. Only five forms are known, and these appear to be divided among two groups. One, occupying the outer end of the Yucatán Peninsula, is composed of *defensor* and *erythromelas*. The other, which is of present interest, contains *clarki* in Michoacán, *quinquecarinatus* of southern Oaxaca, and *palearis* from the Motagua Valley. All members of the genus are lowlanders and are unknown from elevations above 500 m. Though separated by the entire lengths of the Grijalva and Negro valleys and by the interior basins of central Guatemala, there can be no question as to the very close genetic affinities of *palearis* and *quinquecarinatus*. Previous geographic continuity through the corridor will be shown to be the best explanation of the extant condition.



Map 6

Cnemidophorus sacki motaguae Sackett
(Map 6)

The status of this form is still somewhat problematic. Smith and Taylor (1950: 181) considered *motaguae* a synonym of *bocourti*. With this conclusion I do not agree. From the scanty material available from Oaxaca and the abundant material available from Chiapas and Guatemala, it seems fairly certain that the former has a much lower femoral pore count than the latter. I am inclined, therefore, to retain the name *motaguae* for populations south of the Isthmus of Tehuantepec and to restrict the name *bocourti* to those occurring north of the Isthmus.

Cnemidophorus sacki motaguae shows considerable discontinuity in its range. Known from the vicinity of Tuxtla Gutiérrez in the middle Grijalva Valley, it does not make an appearance again until it is encountered in the gorge of the Río Negro and the Salamá Basin of central Guatemala. Throughout the middle valley of the Río Motagua and over the southeastern uplands of Guatemala it is abundant up to an elevation of about 1000 m. Though I have made an intensive search for it at elevations near the 1000 m. contour in the upper valley of the Grijalva and in the Cuilco Valley, I have not encountered it in those regions. At no place between Tehuantepec and El Salvador does it occur along the Pacific versant.

Aside from *bocourti* and possibly other forms farther to the north, *motaguae*, though only one of a number of races of *sacki*, appears to have no immediate affinities in southern Mexico. Certainly, it seems to have little in common with *angusticeps* from the outer end of the Yucatán Peninsula. No other representative of the *sacki* group is known from the lowlands of the Yucatán Peninsula to the south of the subhumid outer parts of the peninsula. This form, though undifferentiated at either end of the corridor, displays a geographic pattern similar to that obtaining in *Enyaliosaurus*.

Leptodeira rhombifera Günther

Though the following may further confuse an already badly confused concept of *Leptodeira rhombifera* and *L. maculata* (Hallowell), it is, nevertheless, necessary to present here some thoughts I have had for some time which are of pertinence not only as concerns the desert corridor but also concerning the relationships of these two species. Dunn (1936) considered *maculata* a race of *septentrionalis* and accorded full specific status to *rhombifera*. The only characters he presented for the separation of the two were (1) the presence of a dark nape stripe in *rhombifera* and the absence of the same in *maculata*, and (2) the more ventral extension of the dorsal rhombs in *maculata* as compared with *rhombifera*. Taylor (1938: 337-42) has shown this last character to be variable in *maculata* and hence untenable as a character for the separation of the two forms. He has shown further that *maculata* and *septentrionalis* are distinct species with overlapping ranges, and other of his data suggest that *maculata* may be vicariously represented by subspecies in various parts of its extensive range. He did not consider *rhombifera* since that form does not occur in Mexico.

Geographically, *maculata* presents a really difficult problem. Although the type was described from Tahiti, it is now generally agreed that it could not have originated from that island. Various suggestions attribute it to Costa Rica or, more probably, to Nicaragua. The type of *maculata* is said to possess a single preocular and possibly one postocular. Taylor (1938) stated that two preoculars are almost invariable in the Mexican form now known as *maculata*,as is true in all of the large series of *rhombifera* known to me. Two postoculars are invariable in *maculata*, and, though I have seen occasional *rhombifera* with three, I have no record of any specimen with only one. Aside from the type and a series of six specimens in the Museo Nacional de Costa Rica which are merely presumed to have stemmed from that country, rather extensive collecting has failed to reveal *maculata* south of San Ricardo in the Grijalva Valley and Tonolá, Chiapas, on the Pacific versant. Taylor (1951: 126) hesitated to accept Costa Rica as the source of the six *maculata* in the Costa Rican museum, and I certainly concur with his opinion. These facts, it seems to me, argue that either the *maculata* of Hallowell is not the form to which that name is currently applied, or the type did not stem from lower Central America.

The very close resemblance of *maculata* to *rhombifera* suggests genetic relationship between the two. Apparently, only the nape stripe presents a diagnostic character for separation, and Taylor (1938: 341) noted that a specimen identified as *maculata* and stemming from Asunción, Chiapas (Grijalva Valley), actually has the nape stripe characteristic of *rhombifera*. In my opinion, the two belong to the same species group, and I would not be surprised if future investigation were to prove them to be subspecies.

Leptodeira rhombifera is known from the dry interior valleys of Central Guatemala southward across the southeastern highlands of Guatemala and along the Pacific versant from extreme eastern Guatemala to Panama. It is unknown from the wetter parts of the Pacific versant of eastern Chiapas and western Guatemala, collecting in both regions having been quite thorough. Neither is it known from the lowlands of the Yucatán Peninsula. Throughout its range it is unknown from elevations above 1000 m.; thus, *maculata* and *rhombifera* have distributions not very different from those of *Sceloporus variabilis variabilis* and *olloporus*.

Though the six groups given above constitute the best herpetological indicators of the corridor, there are several other forms which, though still too imperfectly known to be definitely assigned to this scheme, possess suggestive distributions. Most striking is the distribution of the *pulcher* group of *Conophis*. The typical form, *pulcher pulcher*, though described from "Verapaz, near the Petén" in Guatemala, has since been taken only at Canibal, El Rancho, and Progreso, all within the corridor. This suggests that the form is a dry-land inhabitant and that the types may possibly have originated from the Chisec savannas in northern Alta Verapaz. It has never been taken in a mesic environment. The subspecies *plagosus* is known only from the Pacific versant from eastern Chiapas to El Salvador. There is the possibility, therefore, that the typical form may have passed through the corridor from the chain of savannas that extends from the central part of the Yucatán lowlands into Veracruz, Mexico, or it may have entered the corridor via the Motagua Valley. In either case only the corridor seems to offer an explanation of its occurrence in the middle Motagua Valley and the upper Grijalva Valley. It will probably be shown to be in contact with *plagosus* across the southeastern highlands of Guatemala.

No less suggestive is the distribution of a chain of *Bufo coccifer*-like toads. Typical *coccifer* appears to range from Costa Rica northward into the southeastern highlands of Guatemala. In central Guatemala, at intermediate elevations, it is replaced by an undescribed but obviously related form, and in Guerrero and the Tehuantepec region of Mexico another undescribed but related form occurs. No *coccifer*-like species is known from either the lowlands of the Yucatán Peninsula or the Pacific versant of Guatemala and Chiapas. Again, dispersal through the corridor is indicated.

Aside from the indicator and "near indicator" forms, the herpetofauna of the corridor region is anything but spectacular. Collections to date have revealed that, for the most part, this subhumid area supports at best an impoverished assemblage of wide-ranging xeric types. Some of the more conspicuous of these are *Leptotyphlops phenops phenops*, *Masticophis mentovarius mentovarius*, *Oxybelis aeneus* subsp., *Stenorrhina freminvillei*, *Crotalus durrisus durrisus* among the snakes and *Ctenosaura similis similis*, *Cnemidophorus deppei deppei*, and *Ameiva undulata* subsp. among the lizards.

It may be of some significance that no mesic types are known from the corridor region even though patches of gallery forest not too far removed from humid environments are present, i. e., the gallery forest of the middle Motagua Valley. This would seem to suggest that such mesic conditions are too small and have been too long isolated to support even relict populations of wet-forest forms.

In summarizing the distribution and affinities of the indicators and "near indicators" discussed, several pertinent points must be brought out. First, geographic continuity throughout the length of the corridor can be definitely proved in only one instance. Of the remaining species only *Hypopachus championi* and the *Bufo coccifer* series attain sufficiently high elevations in the oak-pine zone of Guatemala to suggest that they may occur continuously above the dry valleys proper. All the other indicator forms are essentially lowland types, so that geographic continuity in their ranges through the corridor seems improbable.

Second, the closest genetic affinities of the corridor indicators in Guatemala occur not on the lowlands of the Caribbean to the north and east nor on those of the Pacific to the south and west, but rather in lowland areas to the north of the Isthmus of Tehuantepec or along the moderately elevated uplands of Nuclear Central America and along the Pacific lowlands southward. In some instances the same form extends from western Chiapas through the corridor and then southward at least into El Salvador, e.g., *Cnemidophorus sacki motaguae*, which is represented by *Cnemidophorus sacki bocourti* north of the Isthmus of

Tehuantepec. *Sceloporus variabilis* shows much the same pattern except that the typical form extends northward into Tamaulipas, but *olloporus* continues southward into Costa Rica along the Pacific versant. The affinities of *Enyaliosaurus palearis,* as indicated, are not the forms occurring on the Yucatán Peninsula, but, rather, *quinquecarinatus* and *clarki* of Tehuantepec and Guerrero, respectively.

Third, there appears to be no consistency in the differentiation levels in the various populations of the indicator forms in the corridor. It has been noted that *Cnemidophorus sacki motaguae,* though discontinuous in its distribution, has remained undifferentiated throughout the length of the corridor. In contrast, *Sceloporus variabilis,* continuous in its distribution, has split into different races on either side of the main break in the corridor in the Huehuetenango region; *Sceloporus carinatus* and *Sceloporus squamosus*, noncontinuous in their ranges, have differentiated to the specific level.

DISCUSSION

In the Introduction it was noted that a search for a subhumid corridor through northern Central America was initiated by observation of extremely tenuous continuities or discontinuities in the geographic distribution of certain herpetological elements that are essentially dry-land inhabitants. I am concerned, therefore, with the "how," "when," and "where" these conditions were brought about. Three possibilities present themselves. First, there may have been, in the past, continuity in the ranges of certain species through the lowlands of the Yucatán Peninsula. Second, a dry-land corridor may have previously existed along the Pacific versant of northern Central America. And third, the only pathway for dispersal southward for certain dry-land forms (most evidence points to a dispersal from north to south) has been and remains the corridor described herein. To these suggestions may be added the probability of convergent evolution in populations at either end of the corridor, an explanation which, to use the vernacular, would be "making it the hard way."

A route through the lowlands of the Yucatán Peninsula from the Isthmus of Tehuantepec to the middle Motagua Valley would postulate the occurrence of conditions far more xeric than those existing today. True, a chain of savannas from the Veracruz region of Mexico into central El Petén is extant, but as the eastern seaboard is approached these savannas give way to the very wet forests of the eastern parts of the Yucatán Peninsula and of Alta Verapaz. Furthermore, both Ruthven (1912) and Stuart (1935) have given reasons for considering these savannas to be of relatively recent origin. It cannot be doubted, however, that savanna chains similar to those now in existence have at various times wound through the forests of the Yucatán lowlands, if one is to explain certain elements that now occur as isolated populations in local savanna and dry-forest areas on the lowlands. Had the corridor indicators previously made use of such pathways, however, it might well be expected that they or at least their very closest affinities would be present today in such areas. This has been shown to be contrary to fact.

A very similar argument against a Pacific versant corridor obtains. Along the Pacific lowlands from central Chiapas into about central Guatemala mesic conditions occur. To the north and to the south of these two points, respectively, the environment becomes increasingly drier. This mesic region has apparently acted as a barrier to the free movement of a number of forms along the Pacific lowlands, and it is in this general area that a faunal break occurs. A discussion of this point will be presented by me in a forthcoming account of the herpetofauna of the Pacific versant of Guatemala. Of the several indicator species *Sceloporous squamosus* and its relative *Sceloporus carinatus* come closest to completing a distribution circle through the corridor, around the Mexican Sierra Madre to the north, the Guatemalan highlands to the south, and along the Pacific versant. Had previous continuity in the ranges of *carinatus* and *squamosus* existed along the Pacific lowlands, it would certainly be necessary to postulate far more xeric conditions in the past than exist now. As will be shown, such a postulate seems highly improbable.

Only the corridor is left, then, to serve as a pathway for the dispersal of the indicators mentioned. Insofar as the indicators are concerned, all evidence seems to point to a dispersal from north to south. This evidence is twofold. In the groups that have been studied intensively, especially *Sceloporus* and *Cnemidophorus*, there can be little doubt that genetic relationships of the corridor forms center either in the Tehuantepec isthmian region or farther north on the Mexican Plateau. Ecologically, moreover, all the indicators belong to groups that are essentially dry-land types. Suitable environments for these are abundant north of the Isthmus of Tehuantepec but are rare and most probably of relatively recent origin to the south.

To account for the present-day discontinuity in the ranges of the indicators, it seems hardly necessary to go back any further than the Pliocene, during which, from all available evidence, the corridor began its history. The guarded statements of Olsen and McGrew (1941) lead one to believe that northern Central America during the lower Pliocene was probably a rolling upland, fairly warm and humid, and supporting a cover of rain forest and scattered grasslands or forest-margin vegetation. The orogenic movements of the Pliocene which changed the topography of all of northern Central America initiated the development of the corridor. The rising of the Mesa Central of Chiapas, the Sierra de los Cuchumatanes, the highlands of Alta Verapaz, and the Chuacús - Minas-Mico range of Guatemala certainly must have produced rain-shadow conditions in the corridor at a fairly early date. As the highlands increased in elevation to the present time (indeed uplift continues) this rain- shadow condition must have become more and more intense. Though it is certain that there were periods of dry conditions at various times during the Pleistocene, there are no data to indicate that northern Central America was at any time drier than it is today. Certainly, any pronounced aridity would have brought about extinction of the many ancient, mesic amphibian and reptilian types that are now so conspicuous a feature of the herpetofauna of the lowlands of the Yucatán Peninsula. Indeed, if the Sangamon may be taken as an indicator of conditions during interglacial stages, a climate even more mesic than that of today probably existed in that region (Hibbard, 1952, and van der Schalie, 1953). In the corridor region, however, the high mountain barriers between it and the sources of moisture must have ensured continuously xeric conditions.

Thus, it is indicated that dry-land types probably entered the corridor shortly after its formation had begun. As uplift continued, first one species and then another was broken into populations isolated one from another by highland breaks in the corridor.

The several differentiation levels that are now encountered in the indicators have resulted from internal factors of the animals themselves, especially temperature and humidity tolerances, motility, and fecundity. Thus, *Enyaliosaurus*, restricted to elevations below about 500 m. and to the most xeric environments, was the first to be divided into isolated populations which differentiated to the specific level, i. e., *palearis* in the middle Motagua Valley and *quinquecarinatus* on the Pacific side of the Isthmus of Tehuantepec. The prototype of *Sceloporus carinatus* and *squamosus*, apparently tolerant to temperatures of elevations up to 1000 m., would have split somewhat later but still early enough to permit specific differentiation at either end of the corridor. *Cnemidophorus sacki*, though attaining elevations of no more than 1000 m., is representative of a form of high fecundity and of far greater motility (or vagility, if I understand the term) than either *Sceloporus carinatus* or *Sceloporus squamosus* and has remained undifferentiated in the corridor region. *Sceloporus variabilis*, though probably continuous in its distribution, is possessed of rather low vagility, and distance alone appears to have enhanced subspecific differentiation at either end of the corridor. *Hypopachus*, though ranging into relatively high elevations, has similarly been effected by distance and by its short period of activity during the breeding season. It is represented by different species, *maculatus* and *championi*, at either end of the corridor.

On the other hand, it is difficult to explain why certain species have not made use of the corridor. For instance, *Conophis vittatus*, though recorded from the Grijalva Valley, has not managed to invade the corridor in Guatemala. It is entirely possible that other elements will fit into the situation outlined above once the corridor has been more thoroughly studied and the relationships of many forms are better understood.

To what extent other groups of animals have made use of this corridor is at present unknown. The fact remains, however, that a subhumid environment of considerable age linking the dry-lands of southern Mexico with those of northern Central America has been available. If essentially dry-land types in other animal groups show geographic discontinuity or near discontinuity through Guatemala, Honduras, El Salvador, and farther south, it is feasible to assume that they have made use of the corridor in the absence of suitable environments along either the Pacific or Caribbean mesic lowlands.

SUMMARY

Observed discontinuities in the distribution of certain amphibians and reptiles through the dry-lands of southern Mexico and central and eastern Guatemala led me to search for a subhumid corridor between the the Isthmus of Tehuantepec and the deserts of eastern Guatemala and northern Honduras.

Such a corridor was found through the valley of the Río Grijalva of Chiapas and those of the Negro and Motagua of Guatemala. This corridor is comprised of valleys lying for the most part below an elevation of 1000 m. but broken by divides that may attain a height of 2000 m. It is indicated that the corridor had its origin during the Pliocene when the major topographic features of the valleys were outlined and their subhumid climatic conditions were initiated. At present its vegetation cover varies from savanna to desert shrub but in no part could it be termed mesic.

It is believed that herpetological indicators such as certain closely related species, subspecies, or populations in the genera *Hypopachus*, *Sceloporus*, *Enyaliosaurus*, *Cnemidophorus*, and *Leptodeira* could have reached the subhumid lands of Honduras, Guatemala, and the Pacific versant of lower Central America only through this corridor. The absence of closely related forms and the presumedly continuously mesic environments on the lowlands of the Pacific and Caribbean versants between the Isthmus of Tehuantepec and southeastern Guatemala argue against migrations of dry-land forms through those lowland areas.

The biogeographic implications of this subhumid corridor are still extremely vague. Further explanation of the various differentiation levels attained by herpetological elements at either end of the corridor must be sought, and the reasons for the inability of many other groups to have made use of the corridor must be given consideration.

LITERATURE CITED

DUNN, EMMETT R.

1936 Notes on North American Leptodeira. Proc. Nat. Acad. Sci., 22, 12: 689-98.

GOLDMAN, EDWARD ALPHONSO

1951 Biological investigations in Mexico. Smithson. Misc. Coll., 20: 1-476 + xiii, Pls. 1-70, Frontis., 1 map.

GOLDMAN, EDWARD A., and ROBERT T. MOORE

1945 The biotic provinces of Mexico. Journ. Mammal., 26, 4: 347-60, 1 map.

HARTWEG, NORMAN, and JAMES A. OLIVER

1940 A contribution to the herpetology of the Isthmus of Tehuantepec. Misc. Publ. Mus. Zool. Univ. Mich., 47: 1-31.

HIBBARD, CLAUDE W.

1952 New Pleistocene interglacial (Sangamon?) local fauna from Kansas and its climatic significance (Abstract). Bull. Geol. Soc. Amer., 63: 1262.

KÖPPEN, W.

1923 Die Klimate der Erde. Berlin and Leipzig: Walter de Gruyter and Co. Pp. 1-369 + vi, Pls. I-VIII, Figs. 1-25.

MIRANDA, FAUSTINO

1952 La vegetación de Chiapas. Departamento de prensa y turismo, Tuxtla Gutiérrez. Primera parte, pp. 1-334, Figs. 1-94, 2 maps.

OLSEN, EVERETT C., and PAUL O. McGREW

1941 Mammalian fauna from the Pliocene of Honduras. Bull. Geol. Soc. Amer., 52: 1219-44, Pls. 1-4, Figs. 1-5.

RUTHVEN, A. G.

1912 The amphibians and reptiles collected by the University of Michigan-Walker Expedition in southern Vera Cruz, Mexico. Zool. Jahrb., 33, 4: 295-322, Pls. 6-11.

SAPPER, CARL

1894 Gründzuge der physikalischen Geographie von Guatemala. Petermann's Mitteil., 113: 1-59, 4 Karten.

1932 Klimakunde von Mittelamerika. In: Handb. Klimat., 2 (H): 1-74, Figs. 1-13.

1937 Mittelamerika. In: Handb. Reg. Geol., 8 (4): 1-160, Pls. 1-11, Figs. 1-15.

SCHMIDT, KARL P., and L. C. STUART

1941 The herpetological fauna of the Salamá Basin, Baja Verapaz, Guatemala. Field Mus. Nat. Hist., Zool. Ser., 24: 233-47, Figs. 21-22.

SCHUCHERT, CHARLES

1935 Historical geology of the Antillean-Caribbean region. New York: John Wiley and Sons. Pp. 1-811 + xxvi, Pls. 1-16, Figs. 1-107.

SLEVIN, JOSEPH R.

1939 Notes on a collection of reptiles and amphibians from Guatemala. I. Snakes. Proc. Calif. Acad. Sci.,ser. 4, 23, 26: 393-414, Pls. 37-38.

1942 Notes on a collection of reptiles and amphibians from Guatemala. II. Lizards. *Ibid.*, No. 31: 453-62.

SMITH, HOBART M.

1939 The Mexican and Central American lizards of the genus Sceloporus. Field Mus. Nat. Hist., Zool. Ser., 26: 1-397, Pls. 1-31, Figs. 1-59.

1946 Notas sobre una colección de reptiles y anfibios de Chiapas, Mex. Rev. Soc. mexicana hist. nat., 7, 1-4: 63-74.

1949 Herpetogeny in Mexico and Guatemala. Ann. Assn. Amer. Geogr., 39, 3: 219-38, 1 fig.

SMITH, HOBART M., and EDWARD H. TAYLOR

1950 An annotated checklist and key to the reptiles of Mexico exclusive of the snakes. U. S. Nat. Mus. Bull., 199: 1-253 + v.

STEYERMARK, JULIAN A.

1950 Flora of Guatemala. Ecology, 31, 3: 368-72, 1 fig.

STUART, L. C.

1935 A contribution to a knowledge of the herpetology of a portion of the savanna region of central Petén, Guatemala. Misc. Publ. Mus. Zool. Univ. Mich., 29: 1-56, Pls. 1-4, 1 fig., 1 map.

1943 Taxonomic and geographic comments on Guatemalan salamanders of the genus Oedipus. *Ibid.*, 56: 1-33, Pls. 1-2, 1 map.

TAYLOR, EDWARD H.

1938 Notes on the Mexican snakes of the genus Leptodeira, with a proposal of a new snake genus, Pseudoleptodeira. Univ. Kansas Sci. Bull., 25, 15: 315-44, Pls. 30-34, Figs. 1-7.

1951 A brief review of the snakes of Costa Rica. *Ibid.*, 34, 1: 1-188, Pls. 1-23, Figs. 1-7.

VAN DER SCHALIE, HENRY

1953 Mollusks from an interglacial deposit (Sangamon ? age) in Meade County, Kansas. Nautilus, 66, 3: 79-90.

WARD, ROBERT DeC., and CHARLES F. BROOKS

1936 The climates of North America, First Part: Mexico, United States, Alaska. In: Handb. Klimatol., 2 (J): 1-325 + iv, Figs. 1-52.

Copies of this contribution may be purchased from the University of Michigan Press, Ann Arbor, Michigan. Price, $ 0.75.

PLATES

PLATE I

FIG. 1. Vegetation on the Pacific side of the Isthmus of Tehuantepec near the village of Tehuantepec. This xeric cover is more or less typical of the greater part of the Plains of Tehuantepec, where grazing is the main industry. It is widespread over much of the Pacific versant of southern Mexico and is representative of the environment obtaining at the northern end of the subhumid corridor. The thickets of mesquite with occasional stunted trees are often so dense that penetration is possible only along cattle trails. February, 1953; elevation, about 55 m.

FIG. 2. Subhumid uplands in the vicinity of San Pedro Pinula, Guatemala (about 30 airline km. slightly east of south of El Rancho). This environment type is typical of the southeastern highlands of Guatemala below about 1000 m. and at the southern end of the corridor. A number of species undoubtedly moved across these uplands from the Motagua Valley or vice versa to attain the drier environments of the Pacific versant of lower Central America. The hills in the background support a cover of oak and pine which is the vegetation type of elevations between about 1000 and 2000 m. over most of the southeastern uplands. These hills represent the remnants of the ancient mountain mass that forms the southern slopes of the Motagua Valley. March, 1952; elevation, about 1000 m.

PLATE I

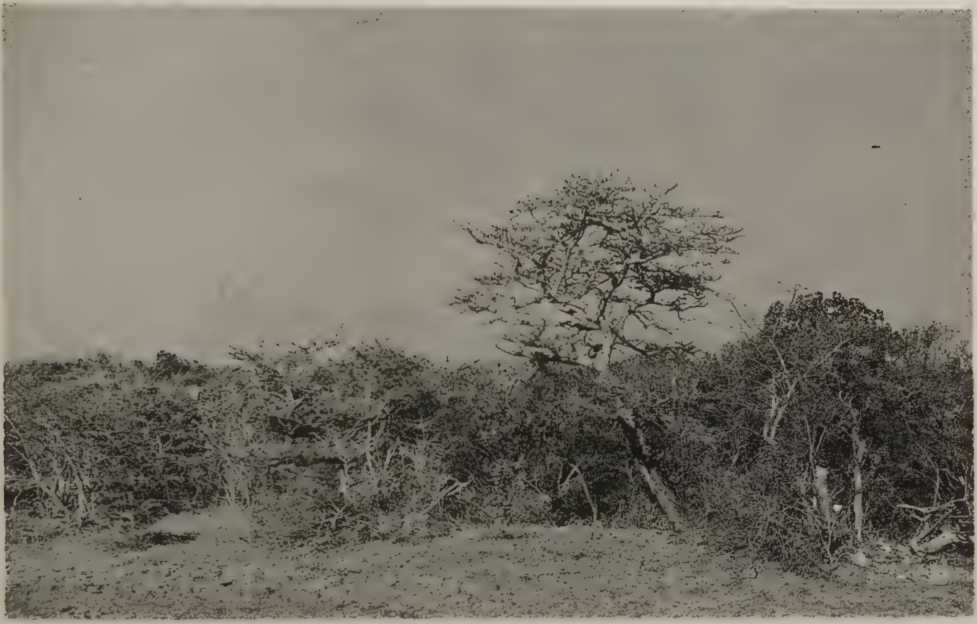


Fig. 1

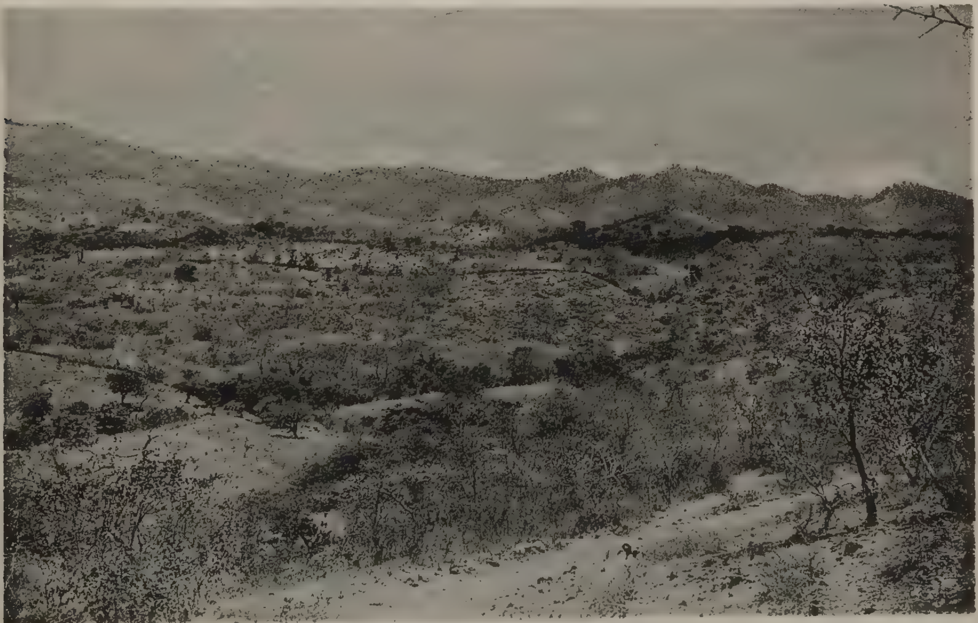


Fig. 2

PLATE II

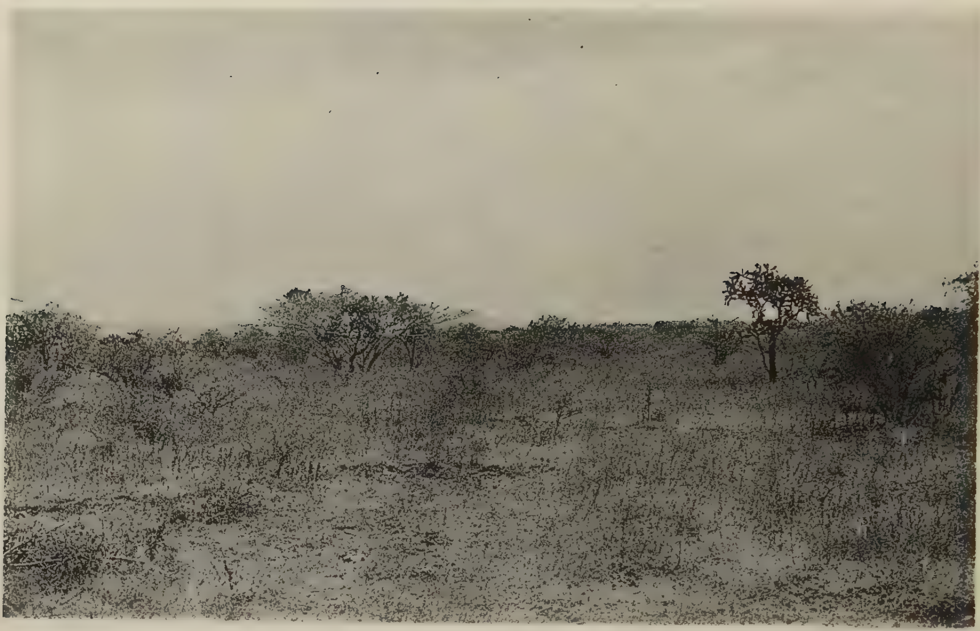


Fig. 1

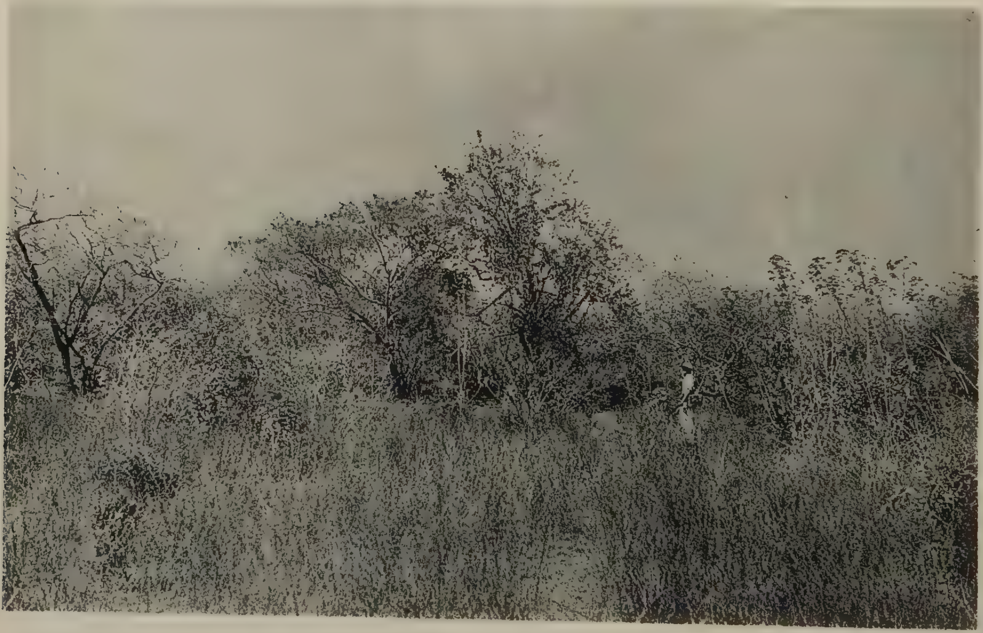


Fig. 2

PLATE II

FIG. 1. Grassy savannas with scattered *nance*, *jicaro*, and cacti in the vicinity of Ocozocoautla in the middle Grijalva Valley. Savannas such as these are the most common vegetation type in the Ocozocoautla-Tuxtla Gutiérrez region. In the left background is the outline of the north face of the outliers of the Sierra Madre. Much of the middle valley of the Grijalva is of considerably higher relief. February, 1953; elevation, about 600 m.

FIG. 2. Savanna and low scrub forest in the upper Grijalva Valley not far from the Guatemalan border and only a few hundred yards from the Río San Gregório. Primarily cattle country, the land is frequently burned over, and the vegetation, though essentially the same as that encountered on the Tehuantepec Plains, is much less dense. February, 1953; elevation, about 800 m.

PLATE III

FIG. 1. Valley of the Río Cuilco (looking downstream) at Canibal on the Mexican border. Note particularly the sparse vegetation on the valley slopes. On the left bank of the stream are groves of planted mango and citrus fruits. Only a single terrace, that on the right bank, is visible, though there are three on the left bank farther upstream. The Sierra Madre is in the distant background. April, 1947; elevation, about 1175 m.

FIG. 2. *Espinal* on a terrace above the flood plain of the Río Cuilco at Canibal is typical of this section of the Cuilco Valley in which the vegetation has been little disturbed by human activities. Note the sparse desert shrub on the valley slope in the background. April, 1947; elevation, about 1175 m.

PLATE III

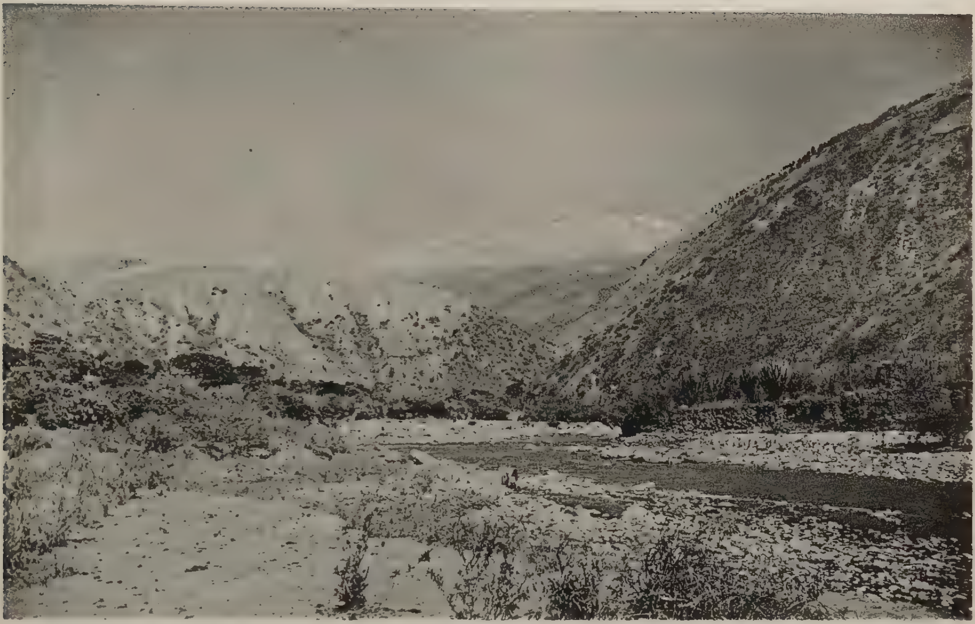


Fig. 1

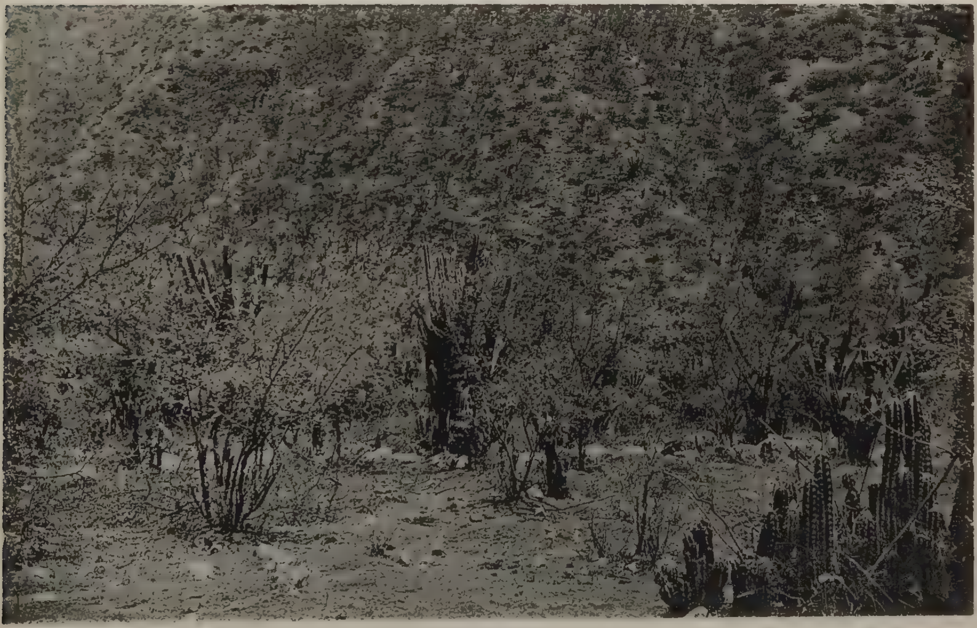


Fig. 2

PLATE IV

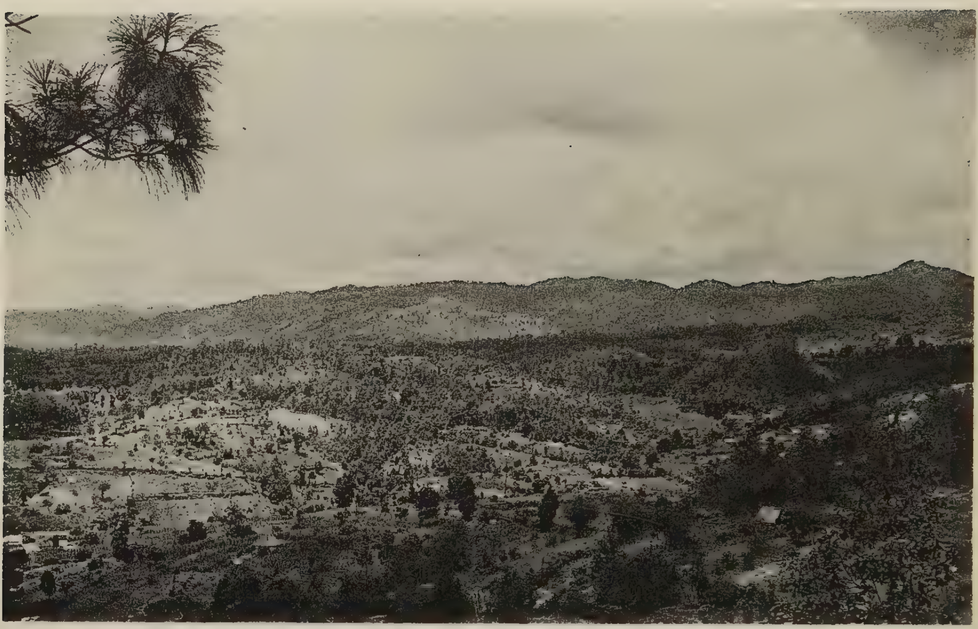


Fig. 1

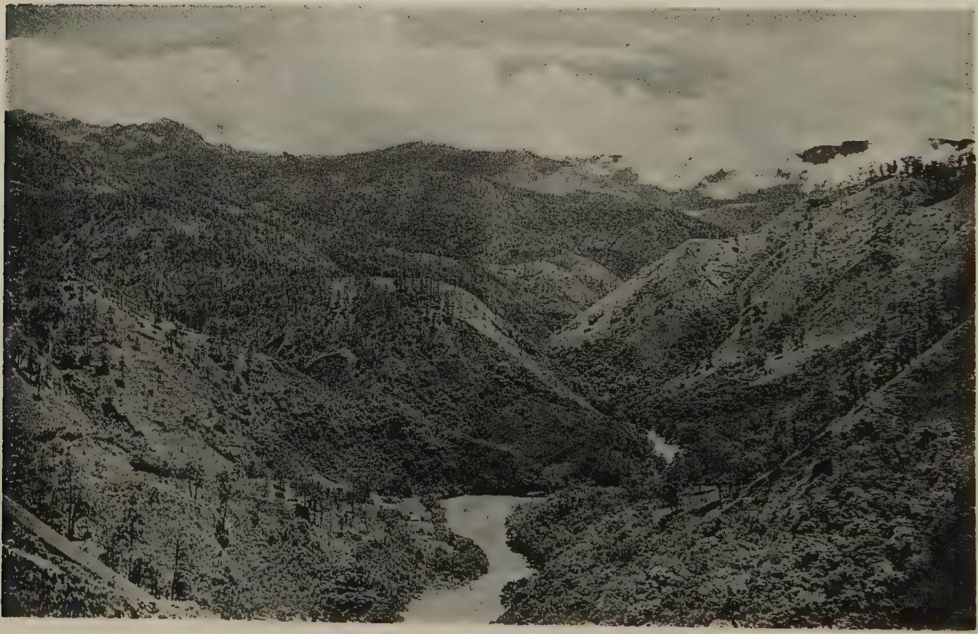


Fig. 2

PLATE IV

FIG. 1. The southwestern highlands of Guatemala on the divide between the watersheds of the Rios Negro and Motagua, looking eastward from the vicinity of Momostenango. Santa Cruz Quiché lies at the base of the ridge in the center background. These rolling uplands are typical of the oak-pine zone on the southwestern highlands and are encountered in the Huehuetenango region, which lies almost due north of the point from which this photograph was taken and which forms the highest break throughout the length of the subhumid corridor. The ridge in the background is the root of the Sierra de Chuacús at its junction with the Guatemalan Plateau. July, 1947; elevation, about 2200 m.

FIG. 2. Valley of the Río Negro at Chixoy below La Primavera, looking downstream with the Sierra de los Cuchumatanes in the background. The narrow valley bottom supports pine savanna, but in this vicinity are occasional thickets of stunted, broadleaf trees, and on the rocky slopes cacti and desert shrubs are not uncommon. Higher in the mountains an open oak and pine forest predominates. Even where clearing has not taken place, vegetation cover in this part of the valley is at best sparse. June, 1940; elevation of river, about 700 m.

PLATE V

FIG. 1. The Salamá Basin near the village of San Jerónimo, looking north. This is typical steppe which is rather heavily grazed. The somewhat denser stand of low trees seen as a thin dark line in the background marks a stream course. July, 1938; elevation, about 950 m.

FIG. 2. The oak-pine zone between the Salamá Basin and the Motagua Valley. The forests of these mountain slopes (north face of the Sierra de las Minas) are open except along the arroyos, where thickets of shrubs occur. Lumbering and grazing have altered somewhat the original cover. The pass between the Salamá Basin and the Motagua lies at about 1400 m. at this point. July, 1938; elevation, about 1200 m.

PLATE V

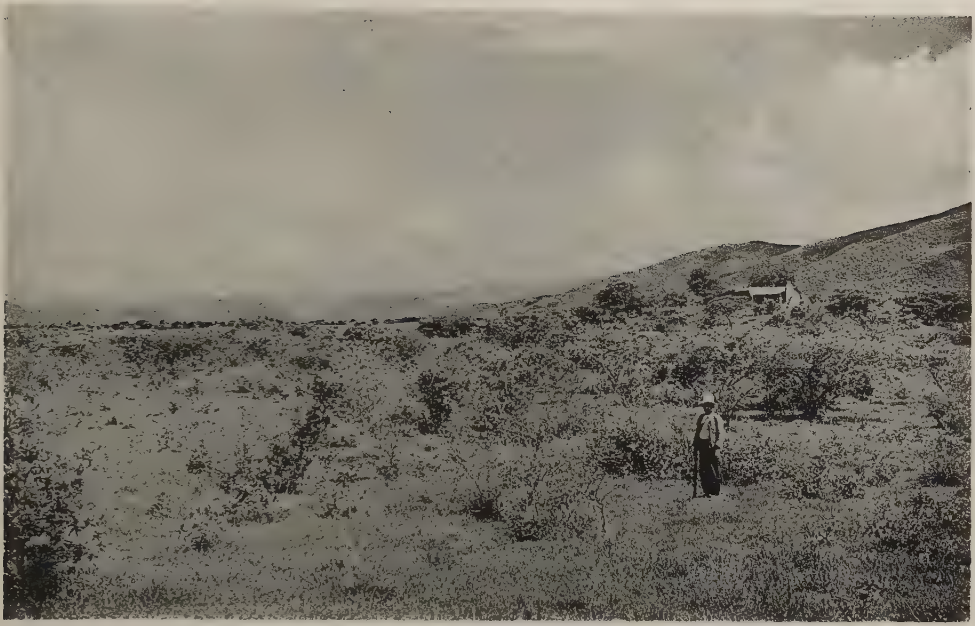


Fig. 1

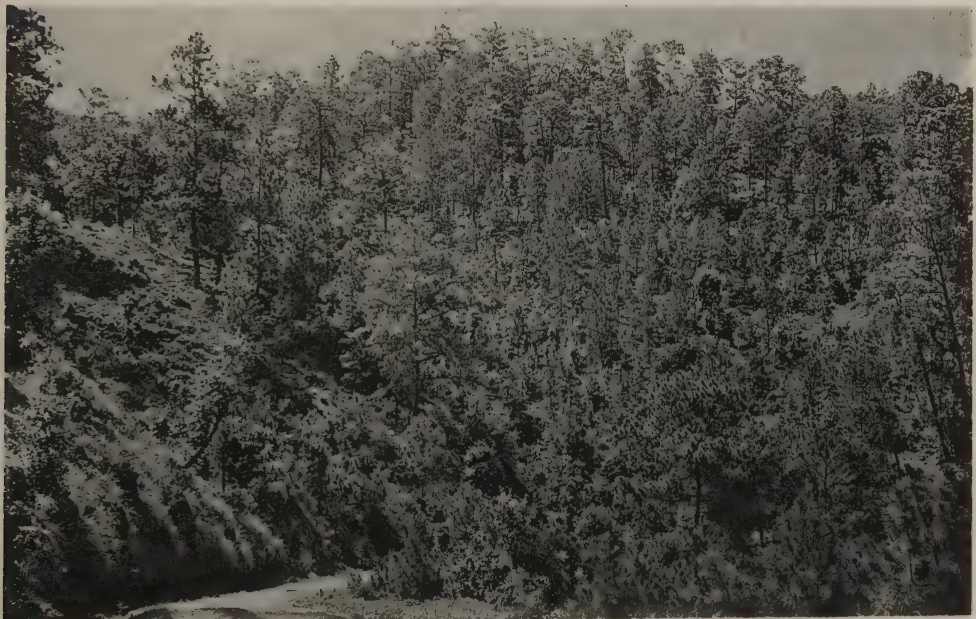


Fig. 2

PLATE VI

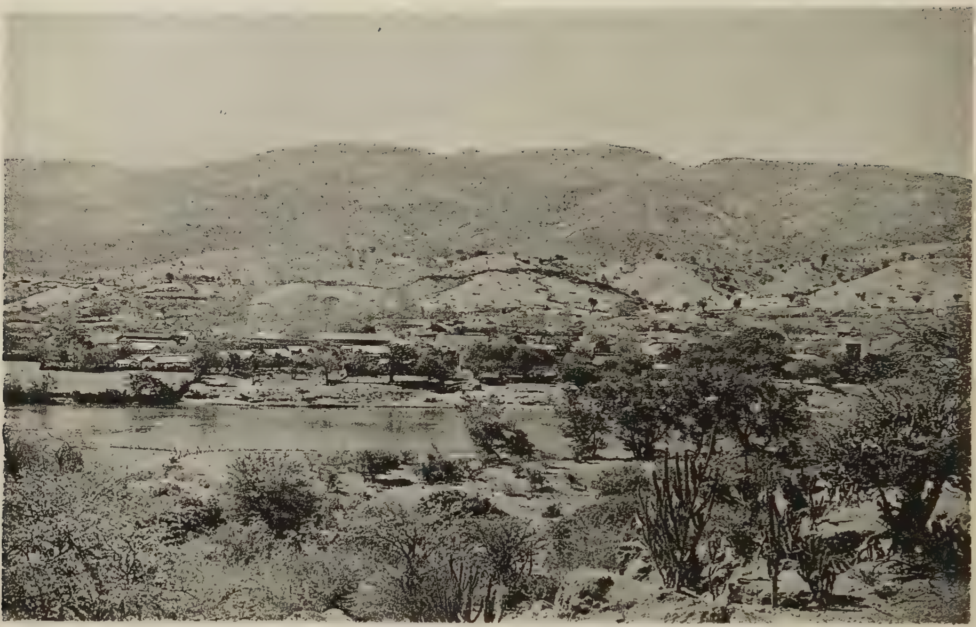


Fig. 1

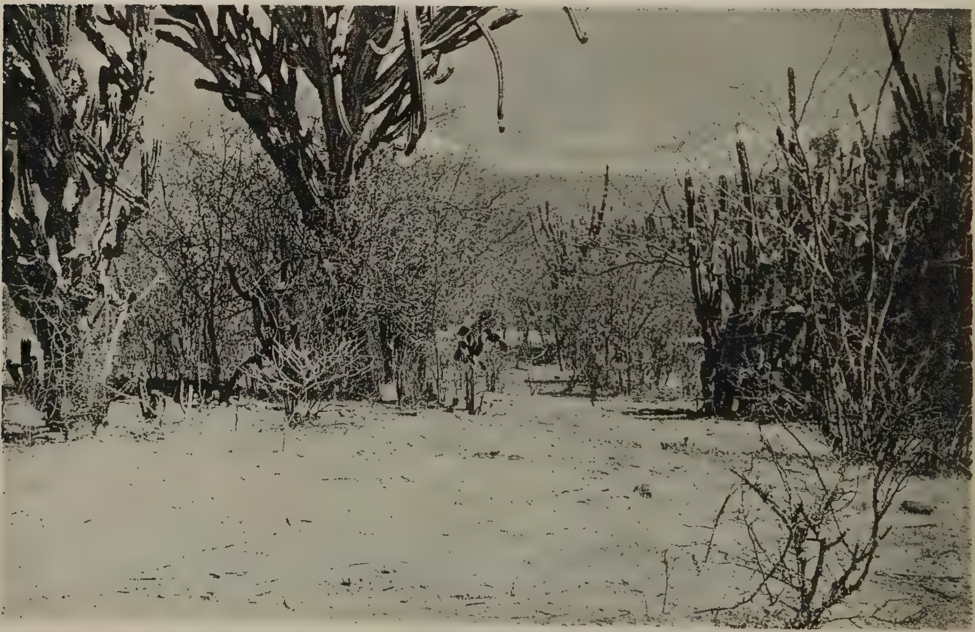


Fig. 2

PLATE VI

FIG. 1. The Motagua Valley at El Rancho, looking south. This is a typical desert landscape that prevails in this part of the valley. Two well-defined terraces are visible; one appears behind the village in the right background, and the village itself is situated on a lower one. Note particularly the sparse cover on the valley slopes in the background. February, 1952; elevation of El Rancho, 275 m.

FIG. 2. Cactus and mesquite flats in the vicinity of El Rancho. The giant cacti are the most conspicuous vegetation features of this part of the valley. Though in places the *espinal* is much denser than shown here, this is the more typical condition. The south face of the Sierra de las Minas is visible in the background. February, 1952; elevation, about 300 m.

596.05 M62C NO 51 65 19>

a39001 007201703b